

Animating the Carbon Cycle: Assessment of the Potential Role of Pumas, Jaguars, White-tailed Deer, and Collared Peccaries in Controlling Carbon Capture and Storage in Mexican Dry Tropical Forest Ecosystems

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Abstract

This report presents estimates of the potential for conserving the top carnivore species (jaguar and puma), their herbivore prey species (white-tailed deer and collared peccary) and their interdependencies and trophic interactions to boost carbon capture and storage within tropical dry forests of Mexico in which all species are resident. The estimates come from deploying a new carbon cycle model that accounts for the direct and feedback effects of animals (consumption, respiration, and nutrient and carbon recycling) on net carbon capture and storage in plant, soil, and animal ecosystem compartments. The model was parameterized with published data based on ecological field studies of typical forest and related shrubland habitat in tropical dry forest ecosystems of central and southern Mexico. The model was solved for steady-state conditions (i.e., a balanced carbon budget) for three scenarios (1) a comparative baseline that excludes both animals; (2) a scenario that includes only the herbivore species; and (3) a scenario that includes the herbivore and predator species. The modeling reveals that conserving these species and their trophic interactions could increase carbon capture and storage by 3.2 times (range 1.68 - 4.7 times) above the level of ecosystem capture and storage in their absence. Considering the predator and prey species and vegetation together as a fully intact food web yields an estimated average yearly net ecosystem carbon capture and storage of 5.68×10^5 kg C per km² per yr or 568 tonnes C per km² per yr. Extrapolating the model estimates to the 18,389 km² of Mexican dry tropical forests already safeguarded in parks and protected areas within Mexico that could support puma and jaguar home range needs reveals a potential to capture and store 10.4 million tonnes C per yr, or 38.3 million tonnes CO₂ per yr. Thus, if conservation acted to ensure that the top predator and large herbivore community of pumas, jaguars, white-tailed deer, and peccaries are restored and protected to exist at their natural densities their impacts on carbon storage across Mexico's tropical dry forest parks and protected areas could reach a level equivalent to $\sim 1/10^{\text{th}}$ of Mexico's 2023 CO₂ emissions from fossil fuel burning.

Keywords: animal-driven carbon dynamics, ecosystem carbon capture, food webs, trophic interactions

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Introduction

Scientists, policymakers, and conservation practitioners are confronted with the dual challenge of mitigating climate change and biodiversity loss.^{1,2} Solutions to each have tended to be treated independently; yet this line of thought is shifting.^{1,3} Growing evidence shows that animals especially may play an essential role in protecting against and mitigating climate change by influencing carbon capture, storage, and protection in ecosystems. Hence, there may be considerable potential congruence between overcoming the biodiversity and climate challenges together.^{3,4,5} Thus, focusing landscape conservation on merely protecting animal populations and diversity without considering their potential impacts on carbon capture and storage could miss opportunities to address the dual challenge.⁶

One promising conservation strategy to address both challenges is known as animating the carbon cycle through trophic rewilding. Animating the carbon cycle (ACC) recognizes that animals, particularly large vertebrates, can have important effects on ecosystem carbon capture despite their smaller total biomass relative to other biological drivers of carbon cycling (e.g., plants or microbes).^{6,7} Trophic rewilding deliberately restores and protects animals in ecosystems with the intention to rebuild intact animal communities, the trophic structure of food webs, and natural ecosystem processes and services for both humans and wildlife.^{8,9}

Estimates derived from a subset of animals across diverse ecosystems reveal that animals could substantially alter an ecosystem's carbon budget by an average of 60 percent to 95 percent, and sometimes more, relative to cases where focal animals are absent, thereby potentially protecting and enhancing ecosystem carbon capture and storage globally by at least 6.4 billion tonnes per year.^{6, 10} By comparison, this global amount rivals that of each of the top five steps identified by the Intergovernmental Panel on Climate Change (IPCC) for reducing net emissions expeditiously, including a rapid transition to solar and wind technology.¹¹

The high potential of ACC to add to the portfolio of nature-based solutions makes it an appealing way to promote wildlife recovery and conservation everywhere to overcome the dual challenges of mitigating climate change and biodiversity loss. However, we are at a juncture where careful examination is warranted if practitioners want to strive for reliable and ecologically accurate biodiversity recovery and protection using ACC.

All species within ecosystems contribute to regulating carbon cycling because of their functional integration into food webs.¹⁰ Yet carbon modeling and accounting still considers only certain subset of functional groups of species (plants, microbes). Growing empirical evidence shows that animal functional groups also matter tremendously. Consequently, many currently proposed natural climate solutions—that do not consider the effects of animals in their modeling and accounting—risk over- or under-estimating the amount of carbon that can be captured and stored in ecosystems. This in turn risks creating inaccurate carbon budgets, which is problematic, in

light of the growing interest to develop nature-based carbon offset payments that could fund the recovery and conservation of animal species and the ecosystems they live in.

We have developed the means to address this problem by developing a new carbon cycle model that can characterize and quantify the effects that animals, both carnivores and herbivores, have as consumers on ecosystem carbon budgets.¹² The model serves as a tool to ascertain the feasibility of using specific on-the-ground trophic rewilding projects to enhance carbon capture and storage. The modeling provides a crucial foundation to assist decision making by conservation aimed at rewilding nature for the purpose of mitigating climate change as well as reversing biodiversity loss.

Here, we report on the application of our model to evaluate the potential for interactions among two dominant predator species (jaguar *Panthera onca*, and puma *Puma concolor*) and their dominant prey (white-tailed deer, *Odocoileus virginianus* and collared peccary *Dicotyles tajacu*) to enhance carbon capture and storage in Mexican dry tropical forests comprised of mixeddeciduous and conifer trees and shrubs.

The Mexican Dry Tropical Forest Ecosystem

Conservation Importance

Mexican dry tropical forests geographically occur along the southwestern Pacific coast of Mexico and in the Yucatan of Mexico.^{13,14} These forests are comprised of stands of oak-pine mixtures or deciduous trees and shrubs that provide food and shelter for a high diversity of animal species. These forest ecosystems provide a variety of ecosystem services in support of human welfare, including provisioning of timber and non-timber forest products; regulating services including sustaining water and air quality, erosion control, temperature regulation and carbon storage; and cultural services including ecotourism, aesthetic and spiritual fulfilment, and employment opportunities.¹⁵ However, these forests are declining in abundance due to deforestation from logging and land transformation for crop and livestock agriculture, thereby jeopardizing the varied ecosystem services, especially carbon storage.¹⁴ Less than 50 percent of the historical area remains as intact dry tropical Forest in Mexico¹⁴, and of the remaining intact forest, only a small fraction (1 percent) is protected.

The Focal Food Web

Carbon storage is considered an important ecosystem service of Mexican dry tropical forests.^{14,16} However, analyses of carbon dynamics do not consider the functional role of animals and their influence on carbon cycling. We focused our analyses on two species of top predator and two species of their large mammalian prey. The predators—jaguar and puma—co-occur throughout these forests and use the landscape space comparatively equally.^{17,18} The dominant prey—for both species are white-tailed deer and collared peccary, which they utilize comparatively equally^{17,18}. White-tailed deer and collared peccary are both browsers, consuming leaves and branches of the shrub layer/habitats within the forest.^{19,20,21} We, therefore, considered the focal

food chain (both consumptive effects and recycling feedbacks) as involving interactions among predators, herbivores and the shrub vegetation (Fig. 1). We assumed that the herbivores did not feed in spatially adjacent mature Forest habitat, using it merely as a thermal refuge and as hiding cover for the prey species (Fig. 1). Hence the only animal impact in the Forest was modeled as a spatial nutrient subsidy that comes from body wastes (urine, feces, carcasses) released in this habitat during parts of the day when the animals resided in this habitat (Fig. 1). The carbon budget was estimated for both Shrub and Forest habitat together.

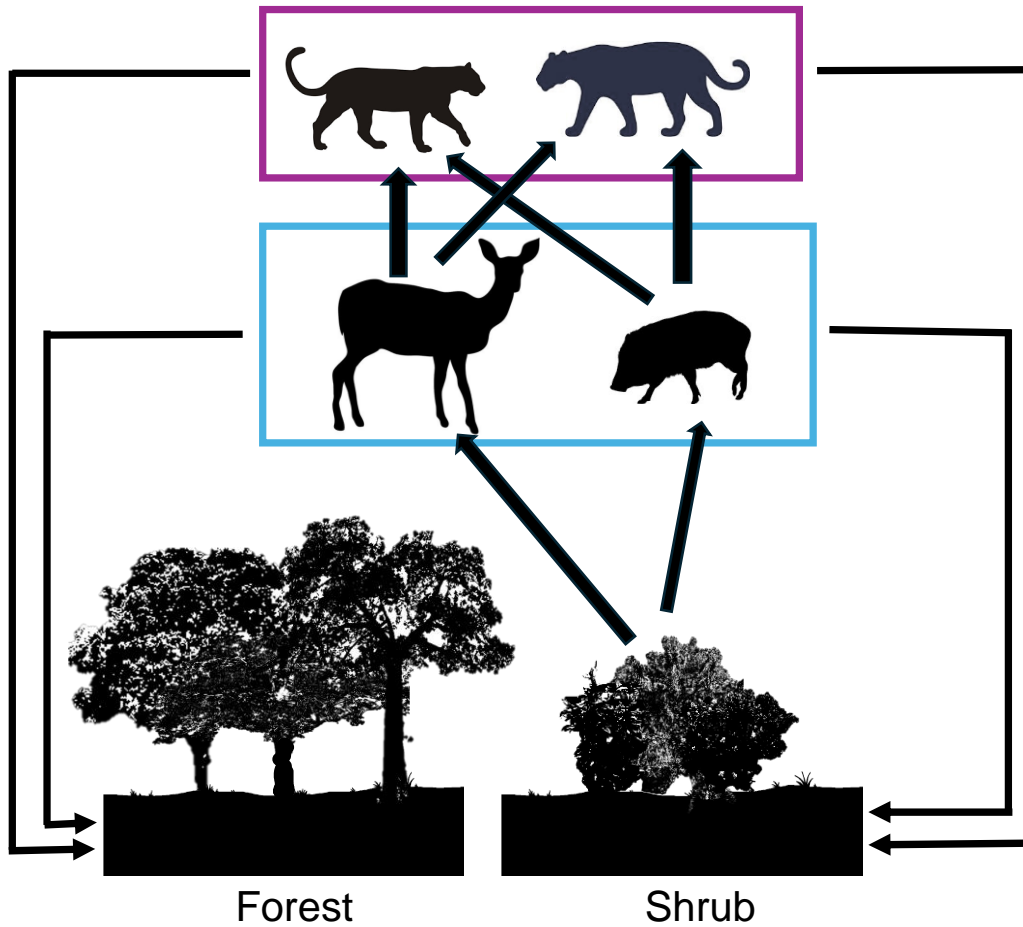


Figure 1. Schematic of the nature of animal effects on Mexican dry tropical Forest ecosystem carbon balance. The figure depicts interactions between top predators (cougar left; jaguar right) and their dominant herbivore prey (white-tailed deer left, collared peccary right) and plants. Upward arrows indicate feeding relations (consumptive effects) between animal consumers and their resources. Downward arrows depict the recycling feedbacks due to animal waste (dung, urine, body carcasses) inputs to the soil. These inputs enhance soil carbon and nitrogen (fertility) status. The modeling assumes that, while herbivores and predators use both Shrub and adjacent Forest habitats, the herbivores derive their nutrition in their diets entirely from foraging in Shrub habitat. Adjacent Forest habitat is assumed to be only used as a thermal refuge by the animals. However, the modeling assumes that animals release some of their body wastes in Shrub habitat while feeding and some in Forest while using that habitat.

Modeling Animal Effects of Ecosystem Carbon Cycling

We modeled the effects of the predator and prey species on standard, accepted components examined when modeling the carbon cycle and when conducting carbon budget estimates. These include gross carbon uptake (gross primary production, GPP), net carbon uptake (net primary production, NPP) and net ecosystem storage potential, aka ecosystem carbon sink strength (Net Ecosystem Carbon Balance [NECB]; see Appendix A.3), of typical tropical dry Forest ecosystems suitable as habitat for the four species to coexist within the landscape. We tailored the general model for the Mexican dry Forest ecosystem to generate estimates of carbon flow and storage in the predators, the herbivore prey, as well as in vegetation in the Shrub habitat (foraging locations for the herbivores and predation areas for the predators) and the tall canopy Forest (thermal refuge for the animals), and in the ecosystem components of the soil (Fig. 1).¹² Further information about the model structure, overarching modeling framework, and R code to run the model used in these analyses are presented in Appendix A.1, with further details available in [12].

A full suite of empirical data values to parameterize the model specifically for any one protected reserve area is not available. Therefore, we used empirical measurements from the published literature for Mexican tropical dry forests in general (see Appendix A.2 for further details). Further, we use data for the predators and prey in Mexico, whenever available to parameterize the relevant model component—however, when data for these species were not available for Mexico, we used data for these species from related ecosystem types.

For both food chains (Forest and Shrub-white-tailed deer-puma; and Forest and Shrub-peccary-jaguar) we modeled the dynamics of the Shrub habitat (in which the herbivores forage and derive their nutrients) using all three model scenarios presented in Rizzuto et al. [12]. Conversely, we modeled the dynamics of the Forest habitat using only scenario (i) from Rizzuto et al. [12], where no animals are present in the model. This was done to capture the ecological reality that, carbon and nutrients stored in Forest biomass are effectively inaccessible to herbivores and, hence, carnivores (as depicted in Fig. 1).

However, the presence of these four animal species can potentially influence the carbon dynamics in the Forest habitat, as well as shaping those of the Shrub habitat, via their nutrient translocation and cycling effects while using both habitats. Thus, we partition the amount of carbon and nitrogen recycled by the animals to represent their potential release between these two different habitats. We partition animal-mediated recycling based on activity data from the published literature that capture the percentage of time spent by either species of herbivores and either species of carnivore in the Forest vs the Shrub portion. For white-tailed deer and peccary, we assume, based on empirical study, that they spend 59 percent of their time in the Shrub habitat and 41 percent in the Forest habitat. For puma and jaguar, we assume equal use (50%–50%) of both habitats.^{17,18, 49,50}

Using the parameter values reported in Table A.1, we ran the model under three competing scenarios: (1) ecosystem carbon uptake and storage in the absence of animals, (2) ecosystem carbon uptake and storage in the presence of herbivores only, and (3) grassland carbon uptake and storage in the presence of both guanaco and puma. By comparing the model's estimates for

these three scenarios, we can estimate the amount of additional carbon that could be gained by conserving just the herbivores, or the herbivores and predators in this ecosystem—that is, the ACC potential of conserving the two groups of animal species within the ecosystem.

We focus on the Shrub habitats of the ecosystem as the source of forage for herbivores and hence sites of predation by the predators based on the assumption that the herbivores will spend about 59 percent of their time in this habitat foraging, and, thus, removing plant biomass C from the ecosystem and returning C as body waste—i.e., feces, urine, and body carcasses resulting from both natural mortality and predation activity of puma and jaguar. We further examine carbon dynamics in adjacent tall canopy Forest based on the assumption that the herbivores and predators will spend about 41 percent of their time in this, thermoregulating and seeking refuge from predation (herbivores) or humans (predators).

Herbivores and predators contribute to carbon capture and storage in the forest by providing spatial nutrient subsidies obtain from the shrubland and released as body as body waste—i.e., feces, urine, that fertilize Forest ecosystem production. We use scenario (1) as a benchmark, simulating a system where no animals are present. Scenario (2) introduces the herbivores to the ecosystem. We ran this scenario after updating the parameters in the model to values that match a scenario with herbivores present in the system (Table A.1). In addition to assigning values to herbivore-related parameters that were set to 0 in scenario (1), we update the values for plant recycling rate (r_P) and carbon loss via plant respiration (δ), as these functional traits of plants change when exposed to herbivory. Note that, in scenario (2), predator-related parameters remain = 0. For scenario (3), we ran the model for a and ecosystem that includes herbivores and predators. Again, we updated some parameter values to account for changes in the functional traits of herbivores when exposed to predation and predation risk. Specifically, we updated the value of herbivore uptake (a_H) and recycling (r_H) rates.

When estimating Net Ecosystem Carbon Balance (NECB) for both habitats, we pro-rate CH_4 emission by herbivores by habitat use. Thus, we subtract 59 percent of herbivore CH_4 emissions from NECB seasonal and yearly estimates for the Shrub habitat, and 41 percent of herbivore CH_4 emissions from NECB estimates for the Forest habitat at the same time scales. We do the same for respiration by herbivores and predators during the non-growing season. For example, to estimate yearly NECB in the Shrub habitat, we subtract 59 percent of herbivore respiration outside of the growing season and 50 percent of the predators' out-of-growing-season respiration. Simultaneously, we subtract 41 percent and 50 percent from the yearly NECB estimate for the Forest habitat, respectively.

This approach allows us to adapt our model to the additional complexity of this ecosystem. The results we present below, then, should be interpreted as first approximations of the potential influence of the four animal species mentioned above on the ability of this tropical Forest ecosystem to capture carbon.

Estimates of Animal-Driven Carbon Sequestration in Mexican Dry Tropical Forest Ecosystem

Appendix A.3 presents the equation used to estimate net ecosystem carbon balance, whereas gross and net primary productivity were estimated using standard approaches. The model provides estimates of all three metrics in units of $\text{kg C m}^{-2} \text{ d}^{-1}$. We scale up our estimates so that they are expressed as $\text{kg C km}^{-2} \text{ growing season}^{-1}$ and $\text{kg C km}^{-2} \text{ yr}^{-1}$ (which includes the wet growing season and dry non-growing season) that can be used to estimate carbon capture and storage across various landscapes in which Mexican tropical dry Forest occurs. We scaled daily estimates to growing season estimates based on an assumed ~120-day wet growing season length for primary productivity. We then extend the estimates for the entire year by assuming that plant and soil processes remain dormant outside of the growing season and debiting continued C loss due to active animal respiration and methane emissions during this non-growing season. Empirical evidence that soil and plant fluxes are very low to dormant in the Shrub and Forest habitat for the dry season outside the growing season supports this approach.⁵¹

Finally, we account for enteric methane (CH_4) emissions from the herbivores during the growing season. As no empirical measurement of white-tailed deer and peccary CH_4 emission exist yet, we used the allometric relationship published in [13] to estimate CH_4 emission for an average 48 kg adult white-tailed deer and an average 15.7 kg adult collared peccary.^{21,39} Table 1 reports the estimates of seasonal ecosystem gross primary productivity (GPP), net primary productivity (NPP), and net ecosystem carbon balance (i.e., carbon capture [NECB]) for the three scenarios. As well, Table 1 presents yearly NECB estimated by debiting animal CO_2 and methane release during the non-growing season when plants are dormant, but animals are still active.

Puma-White-Tailed Deer-Vegetation Food Chain

The modeling analyses reveal that NPP (net carbon capture) in the presence of white-tailed deer (Scenario 2) could be 1.33 x higher than in the no-animal scenario (Scenario 1) for the Shrub habitat, and 1.78 x higher in the Forest habitat (Table 1). Adding pumas (Scenario 3) is calculated to increase NPP by 1.67 x above the no-animal scenario in the Shrub habitat and by 1.78 x in the Forest habitat (Table 1). This indicates that pumas enhance carbon capture in Shrub, above the effect of white-tailed deer alone, but they have no added net effect above white-tailed deer in Forest habitat. Yearly NECB (net carbon storage) in the presence of white-tailed deer is calculated to be 1.38 x higher than in the no-animal scenario for the Shrub habitat and 1.75 x higher in the Forest habitat (Table 1). Adding pumas is calculated to increase NECB to 1.67 x higher than the no-animal scenario in the Shrub habitat, and 1.74 x higher in the Forest habitat (Table 1), indicating that pumas have a net effect that slightly decreases NECB relative to white-tailed deer alone in Forest habitat (Table 1).

Summing the NECB for the two habitats (Table 1) gives net estimates of annual carbon storage for the entire tropical dry Forest ecosystem. The modeling leads to an estimated total of $2.97 \times 10^5 \text{ kg C}/(\text{km}^2 \cdot \text{yr})$ [297 tonnes $\text{C}/(\text{km}^2 \cdot \text{yr})$] in the presence of pumas and white-tailed deer vs. $1.77 \times 10^5 \text{ kg C}/(\text{km}^2 \cdot \text{yr})$ [177 tonnes $\text{C}/(\text{km}^2 \cdot \text{yr})$] in the absence of animals. This amounts to an estimated net 1.68 x increase in total carbon storage due to puma and white-tailed deer effects.

Table 1. Estimated gross primary productivity (GPP), net primary productivity (NPP), and net ecosystem carbon balance (NECB: i.e., carbon capture) for a Mexican dry tropical Forest ecosystem under different scenarios of food chain lengths: (1) the no animal, (2) white-tailed deer-only, (3) white-tailed deer-puma, (2) collared peccary-only, and (3) collared-peccary-jaguar. Seasonal estimates are calculated over an assumed growing season of 120 days. Seasonal, and yearly NECB estimates account for white-tailed deer and peccary methane (CH₄) emissions, and yearly estimates account for animal respiration and white-tailed deer and peccary methane release for the non-growing part of the year (245 days). Note that all estimates are provided on a per-km² spatial scale, to allow extrapolation to broader landscape scales.

	Scenario	Seasonal			Yearly
		GPP kg C km ⁻² 120 d ⁻¹	NPP kg C km ⁻² 120 d ⁻¹	NECB kg C km ⁻² 120 d ⁻¹	NECB kg C km ⁻² y ⁻¹
Shrub	No-animals	2.26 x 10 ⁵	1.64 x 10 ⁵	1.64 x 10 ⁵	1.64 x 10 ⁵
	W-T Deer	3.03 x 10 ⁵	2.17 x 10 ⁵	2.27 x 10 ⁵	2.26 x 10 ⁵
	W-T Deer-Puma	3.03 x 10 ⁵	2.74 x 10 ⁵	2.74 x 10 ⁵	2.73 x 10 ⁵
	Peccary	3.51 x 10 ⁵	1.02 x 10 ⁵	1.05 x 10 ⁵	1.05 x 10 ⁵
	Peccary-Jaguar	9.55 x 10 ⁵	8.17 x 10 ⁵	8.17 x 10 ⁵	8.16 x 10 ⁵
Forest	No-animals	1.79 x 10 ⁴	1.35 x 10 ⁴	1.35 x 10 ⁴	1.35 x 10 ⁴
	W-T Deer	2.84 x 10 ⁴	2.40 x 10 ⁴	2.40 x 10 ⁴	2.37 x 10 ⁴
	W-T Deer-Puma	2.84 x 10 ⁴	2.40 x 10 ⁴	2.40 x 10 ⁴	2.35 x 10 ⁴
	Peccary	2.84 x 10 ⁴	2.40 x 10 ⁴	2.40 x 10 ⁴	2.37 x 10 ⁴
	Peccary-Jaguar	2.84 x 10 ⁴	2.40 x 10 ⁴	2.40 x 10 ⁴	2.36 x 10 ⁴

The modeling indicates that at equilibrium the carbon dynamics happen under a mean density of 11.3 white-tailed deer/km² in the absence of puma (Table 2), and 15 white-tailed deer/km² in the presence of puma. Pumas are estimated to occur at a mean density of 0.09 animals/km².

Jaguar-Collared Peccary-Vegetation Food Chain

The modeling analyses reveal that yearly NPP (carbon capture) in the presence of collared peccaries (Scenario 2) is 0.62 x that in the no-animal scenario (Scenario 1) for the Shrub habitat, and 1.78 x higher in the Forest habitat (Table 1). This indicates that peccaries reduce carbon capture in Shrub but enhance it in Forest. Adding jaguars (Scenario 3) is calculated to increase NPP by 5 x above the no-animal scenario in the Shrub habitat and by 1.78 x in the Forest habitat (Table 1). This indicates that jaguars reverse the negative effects of peccaries on carbon capture in Shrub but they have no added net effect above peccaries in Forest habitat. Yearly NECB (net carbon storage) in the presence of peccaries is calculated to be 0.64 x that of the no-animal scenario for the Shrub habitat and 1.76 x higher in the Forest habitat (Table 1). Adding jaguars is calculated to increase NECB to 5 x higher than the no-animal scenario in the Shrub habitat, and 1.75 x higher in the Forest habitat (Table 1), indicating that jaguars have a net effect that slightly decreases NECB relative to peccaries alone in Forest habitat (Table 1).

Summing the NECB for the two habitats (Table 1) gives net estimates of annual carbon storage for the entire tropical dry Forest ecosystem. The modeling leads to an estimated total of 8.4×10^5 kg C/(km² · yr) [840 tonnes C/(km² · yr)] in the presence of jaguars and peccaries vs. 1.77×10^5 kg C/(km² · yr) [177 tonnes C/(km² · yr)] in the absence of animals. This amounts to an estimated net 4.74 x increase in total carbon storage due to effects of jaguars and peccaries.

The modeling indicates that, at equilibrium, the carbon dynamics happen under a mean density of 9.6 collared peccaries/km² in the absence of jaguar, and 13 peccaries/km² in the presence of jaguar. Jaguar are estimated to occur at a mean density of 0.102 animals/km².

Caveats

Estimates of carbon capture across scenarios are highly sensitive to select, key parameters of the model system. In the no-animal scenario, soil respiration and plant recycling rates are key parameters shaping the ecosystem's ability to capture carbon. In the herbivore-only and herbivore-carnivore scenarios, the herbivores' and predators' uptake rates (i.e., intensity of herbivory and predation, respectively) play important roles, in addition to soil respiration and plant recycling, in shaping the estimated carbon capture.

Validating the Estimates

Measurements of predator- and herbivore-driven GPP, NPP and NECB do not exist, so the estimates for scenario (2) and scenario (3) cannot yet be validated. However, the model can be validated by comparing model predictions of predator and herbivore species density against published estimates. As well, net productivity and NECB have been measured in tropical dry Forest ecosystems in the absence of animals, which can be compared against model estimates for scenario (1) with no animals present in the ecosystem.

Herbivore and Predator Species Density

The model estimates white-tailed deer density at 11.3 animals/km² and collared-peccary density at 9.6 animals/km² for the herbivore-only scenario and 15 and 13 animals/km² for the herbivore-predator scenario. These densities are near the range of densities reported throughout Mexican tropical dry Forest regions of 11-13 white-tailed deer/km² and 4-10 collared peccary/km.^{2,52}

The model estimates a puma and jaguar density of 0.09/km² animals and 0.102 animals/km² (Table 2). This is close to density estimates in Mexican dry tropical Forest of 0.027-0.069 puma/km²⁵³ and 0.026-0.054 jaguars/km.^{2,54}

Net Primary Productivity and NECB

Field measurements of net primary productivity (NPP) reveal that tropical dry Forest ecosystems can capture between $2.5 \times 10^5 - 6.25 \times 10^5 \text{ kg C}/(\text{km}^2 \cdot \text{yr})$.^{55,56,57} This range is 1.4 - 3.5 x higher than the modeled total yearly NPP (Shrub + Forest) of $1.77 \times 10^5 \text{ kg C}/(\text{km}^2 \cdot \text{yr})$ for the no-animal scenario in Table 1. Field measurements of NECB reveal that tropical dry Forest ecosystems can store between $1.25 \times 10^5 - 1.53 \times 10^5 \text{ kg C}/(\text{km}^2 \cdot \text{yr})$ ⁵¹, which is 77 percent - 86 percent of the $1.77 \times 10^5 \text{ kg C}/(\text{km}^2 \cdot \text{yr})$ predicted by the modeling for the no-animal scenario 1 (Table 1).

The overall closeness between empirical measures and several of our modeled values gives us confidence that model predictions for the Mexican tropical dry Forest ecosystem are a reasonable first approximation of the ecosystem's carbon dynamics.

Discussion

Tropical dry forests across the neotropics, and especially in Mexico, are among the most threatened of tropical Forest ecosystem types, due to conversion into other human uses including logging and crop and livestock agriculture.¹⁴ Consequently, 48 percent or more of tropical dry forests have been lost across their geographic extent of the southwestern Pacific Coast of Mexico and in the Yucatan of Mexico.^{13,14} Moreover, much of what remains is fragmented to varying degrees. Continued fragmentation will disrupt natural movements of animals, thereby altering food chain interactions and attendant nutrient cycling processes.⁵⁹ Top predators, in these ecosystems, especially, are important for controlling the abundance and activity of prey populations with implications for sustaining ecosystem functions, including carbon sequestration.^{14,58,62} Thus, conservation of tropical dry Forest ecosystems and constituent biodiversity that drives ecosystem processes and services will depend on quantifying the value of protecting existing mosaics of Forest remnants and the extent to which these mosaics can be used as sources for restoration of degraded areas.⁵⁸

To this end, this report presents quantitative estimates that reveal the critical value of protecting ecological food chains comprised of mammalian top predators and herbivores in support of sustaining and enhancing carbon sequestration. The estimates derive from a carbon cycle model designed to explicitly account for the direct and indirect effects of animals on ecosystem carbon capture and storage.¹² The model was parameterized (Table A.1) using data for nutrient and carbon uptake (i.e., foraging, predation) and release and recycling (i.e., urination, defecation, carcass deposition) by top predators (puma, jaguar) and their dominant prey species (white-tailed deer and collared peccary), as well as plant and soil ecophysiology including plant nutrient and carbon uptake (i.e., root uptake, photosynthesis) and recycling (i.e., respiration, litterfall), and soil respiration and nutrient loss (i.e., leaching) for Shrub and forested habitats comprising tropical dry Forest ecosystems.

The modeling examined two independent food chains, one involving puma-white-tailed deer interactions and cascading impacts on Shrub and Forest habitats, another involving jaguar and

collared peccary and their cascading impacts on the two habitats. These species were chosen because they are the dominant top predators in Mexican tropical dry forests and their dominant prey species, with puma preferring white-tailed deer slightly more than jaguar, and jaguar preferring peccaries slightly more than puma.^{18,45} However, each predator also uses the other prey.^{18,45} Indeed, the two predators tend to be functionally similar, with considerable diet and spatial overlap in habitat use with similar home-range sizes.^{17,60,61}

The model estimates for net carbon capture (NPP) and net amount of carbon storage in the ecosystem—i.e., carbon sink strength (NECB)—were validated by means of (i) comparing model estimates of animal population densities to published measures of animal densities in tropical dry forests of Mexico, and (ii) comparing model estimates of net primary productivity (NPP) and net carbon capture and storage (NECB) to published field measurements from Mexican tropical dry Forest ecosystems. Data were available only for study locations where animals were absent (measurement data for cases where animals are present are not yet available). This validation revealed that the model predictions were very close to empirical measures, giving confidence in the reliability of the model estimates.

The modeling revealed that white-tailed-deer presence and their impacts at a predicted equilibrium density of 11 individuals/km² is predicted to increase the capacity of the ecosystem to capture and store 1.77 x more carbon than in their absence (Yearly NECB; Table 1). The presence of puma, at a predicted density of about 0.08 individuals/km² is predicted to increase carbon capture and storage by 1.2 x more than what white-tailed deer are predicted to do alone. This means that when the animals co-occur as an intact food chain, they, together, increase the capacity of the ecosystem to capture and store 1.68 x more total carbon than when they are both absent from the ecosystem.

The modeling results for the jaguar-peccary-vegetation system differed considerably from the puma-white-tailed deer-vegetation system, where, in the latter case, animals consistently enhanced carbon capture and storage. Analyses reveal yearly NECB in the presence of an estimated density of 9.6 collared peccaries/km² is calculated to be 0.64 x that of the no-animal scenario for the Shrub habitat, whereas the effect on Forest (1.76 x higher than in the no-animal case: Table 1) is similar to white-tailed deer. However, adding jaguars at an estimated density of 0.102 animals/km² is calculated to reverse the negative effects of peccaries and increase Shrub NECB to 5 x higher than the no-animal scenario, and 1.78 x higher in the Forest habitat (Table 1). Hence jaguars act to improve NECB overall by 4.7 x above conditions with no animals (Table 1).

Summing the NECB for the two habitats (Table 1) gives net estimates of annual carbon storage for the entire tropical dry Forest ecosystem. The modeling leads to an estimated total of 2.97×10^5 kg C/(km² · yr) [297 tonnes C/(km² · yr)] in the presence of pumas and white-tailed deer. Summing gives an estimated total of 8.4×10^5 kg C/(km² · yr) [840 tonnes C/(km² · yr)] in the presence of jaguars and peccaries. Because the two predators coexist in Mexican dry tropical Forest ecosystem and that they are effectively functionally equivalent, we can reach a first approximation of their total net effects when together in a food web (Fig. 1) by averaging the effects of the two modeled food chains.^{17,18,45,60,61} This gives an estimated average yearly NECB

for the fully intact food web of 5.68×10^5 kg C/(km² · yr) [568 tonnes C/(km² · yr)] which is 3.2 x above conditions with no animals.

The analysis provides estimates for ecosystem carbon capture and storage (NECB) and animal densities on a per km² basis (Table 1). This allows for extrapolation of the model estimates for Mexican tropical dry forests with comparable environmental conditions. As a start, we conducted such scaling for tropical dry forests already protected within Mexico (Table 2). The candidate protected areas, presented in Table 2, are the subset of all Mexican tropical dry Forest protected areas that exceed a minimal spatial extent (> 30 km²) needed to support the puma and jaguar home range needs.⁶³ Thus extrapolating 568 tonnes of carbon capture and storage per year to the total protected area extent of 18,389 km² has the potential to lead to an average net ecosystem carbon uptake and storage of 1.04×10^7 tonnes C/yr [10.4 million tonnes C/yr, or 38.3 Mt CO₂/yr] if conservation acted to ensure that the top predator and large herbivore community of pumas, jaguars, white-tailed deer and peccaries are restored and protected to exist at their natural densities. This amount is about 1/10th of Mexico's 2023 CO₂ emissions from fossil fuel burning.⁶⁴

Table 2. List of Mexican protected areas that are large enough to aid in Animating the Carbon Cycle through conservation of the dominant predator (jaguar, puma) and prey (collared peccary, white-tailed deer) species that can impact the carbon cycle of dry tropical Forest ecosystems.

Park or Biosphere Reserve [†]	Location	Size (km ²)*
Arrecife Alacranes	Yucatán	3337
Bahía de Loreto	S. Baja California	2065
Bahías de Huatulco	Oaxaca	118
El Gogorrón	San Luis Potosí	250
El Veladero	Guerrero	36
La Malinche	Tlaxcala and Puebla	457
Lagunas de Chacahua	Oaxaca	141
Pico de Tancítaro	Michoacán	231
Sistema Arrecifal Veracruzano	Veracruz	522
Volcán Nevado de Colima	Jalisco and Colima	96
La Primavera	Jalisco	305
Sierra de Quila	Jalisco	152
Archipiélago de Revillagigedo	Colima	6366
Chamela- Cuixmala	Jalisco	131
La Encrucijada	Chiapas	1449
Sierra de Manantlán	Jalisco and Colima	1395
Sierra del Abra Tanchipa	San Luis Potosí	214
	Total	18,389

[†] Source: <http://vivanatur.org/BiodiversityConservationANP.html>

* The selected protected areas are $> 30 \text{ km}^2$, the minimum area needed to support the home range of a single jaguar or puma⁶³.

An interesting model prediction is that white-tailed deer density in the presence of predators (~ 15 individuals per km^2) should be $1.32 \times$ higher than the 11.3 individuals per km^2 density of deer in the absence of predators and that collared peccary density in the presence of predators (~ 13 individuals per km^2) should be $1.32 \times$ higher than the 9.6 individuals per km^2 density of peccaries in the absence of predators. From a population biology perspective this may seem counter intuitive because predation is expected to cause fewer prey individuals to exist in a population relative to when predation is absent.⁶² However, the effect is a consequence of the top-down ecosystem control by predators and herbivores causing recycling feedbacks that enhance forage productivity for the prey. This effect may be especially apparent in this system which has comparatively low productivity and is consistent with predictions from the general model.¹² Moreover, existing theories of ecosystem assembly and structure indicate that food chain length can only increase if primary productivity increases.⁶⁵ Hence, what may be happening here is that the puma and jaguar may be engineering their ability to be part of the ecosystem via their feedback effects that enhance primary productivity of this comparatively unproductive system sufficiently enough that the herbivores can reach densities high enough to support the predator populations. This highlights the existence of an important yet delicate balance that is attained in this ecosystem once the food chain becomes established.

Our analysis is simplistic because it focuses on a few dominant mammalian predators and prey in Mexican tropical dry forests. However, these forests contain a wide diversity of animals species.^{17,18,58,62,63} Thus, there may be additional food web interactions that could lead to reductions in ecosystem carbon capture and storage, given that some animal species could have negative effects on ecosystem carbon dynamics.^{7,10} Indeed, we predict that peccaries should have a negative effect in the Shrub habitat in which they are assumed to source all of their food. But the analysis shows that this effect can be obviated in the presence of predators.

The analysis also does not consider climate effects on carbon dynamics. Indeed, empirical research has shown that precipitation conditions outside and within the growing season could alter carbon dynamics and, depending on precipitation levels, could overwhelm biotic processes and cause Mexican tropical dry Forest ecosystems to rapidly shift from being carbon sinks to carbon sources.⁵¹ This underscores the fragility of ecosystem functions of these systems, which, as our analyses show, can be exacerbated by loss of animal tropic structure in the ecosystem. This further underscores the need to consider climate change and animal conservation synergistically, and accordingly consider the potential for intact food chains to help create resilience to climate change.⁶

In conclusion, the model analysis revealed that enhancing the conservation of pumas, jaguar, white-tailed deer, and peccaries as an intact functioning food web could enhance net ecosystem carbon storage by an estimated 3.2 times above what would be captured and stored in their absence (Table 1). Of course, the actual performance of the ecosystem to capture and store carbon will have to be monitored and verified at the site using animal exclosure studies. Regardless, the analyses support considering the promotion of conserving these wildlife species within Mexican tropical dry Forest parks and protected areas as a feasible nature-based climate solution.

Appendices

A.1 The Model's Equilibrium Solutions.

We modeled this case study using the equilibrium solutions (i.e., an ecosystem balance) for each of the three modeling scenarios in [12]: (1) carbon uptake and storage in the absence of animals (Box 1.1); (2) carbon uptake and storage in the presence of herbivores (Box 1.2); and (3) carbon uptake and storage in the presence of herbivores and predators (Box 1.3). The ecosystem model version that we used includes a food chain comprising four compartments: soil, plants, herbivore, and predator. For each of these compartments, the model tracks gains (e.g., inorganic inputs, nutrient uptake, photosynthesis) and losses (e.g., leaching, respiration, recycling). At the ecosystem level, the model estimates gross and net primary productivity and net ecosystem carbon balance (NECB). NECB captures the net accumulation of carbon in ecosystems.³⁰ In measuring NECB, we use an expanded formula that accounts for the direct and indirect effects of animals on ecosystem carbon cycling (see Appendix A.3 and [12] for more details). **The R code to run the analyses described in this report is available upon request.**

Box 1.1: The soil-plant model equilibrium of scenario (1)

The set of equilibrium solutions for scenario (1) from [12] is,

$$Soil_N = \frac{I}{k} \quad (A.7)$$

$$Soil_C = \frac{kr_P}{a_p I} \quad (A.8)$$

$$Plant_N = \frac{q_S}{a_p \alpha (1 - \delta)} \quad (A.9)$$

where N stands for nitrogen and C stands for carbon. See Table A.1 for a short description of parameters, and [12] for a more detailed one. As the model described in [12] uses the C:N to track the budget and cycling of C in the ecosystem, plant C content is recovered as,

$$Plant_C = \alpha \cdot Plant_N \quad (A.10)$$

ⓘ Box 1.2: The soil-plant-herbivore model equilibrium of scenario (2)

The set of equilibrium solutions for scenario (2) in [12] is,

$$Soil_N = \frac{I}{k} \quad (A.1)$$

$$Soil_C = \frac{kr_H r_P (\alpha(1 - \delta) + (\pi - 1)\beta)}{I(a_H q_S + a_P (\pi - 1)\beta r_H)} \quad (A.2)$$

$$Plant_N = \frac{r_H}{a_H} \quad (A.3)$$

$$Herbivore_N = -\frac{r_P (a_H q_S + a_P r_H \alpha (\delta - 1))}{a_H (a_H q_S + a_P (\pi - 1)\beta r_H)} \quad (A.4)$$

where N stands for nitrogen and C stands for carbon. A brief description of parameters can be found in Table A.1, and a more detailed one in [12]. As the model described in [12] uses the C:N to track the budget and cycling of C in the ecosystem, plant and herbivore C content are recovered as,

$$Plant_C = \alpha \cdot Plant_N \quad (A.5)$$

and

$$Herbivore_C = \beta \cdot Herbivore_N \quad (A.6)$$

① Box 1.3: the soil-plant-herbivore-predator model equilibrium of scenario (3)

The set of equilibrium solutions for scenario (3) in [12] is,

$$Soil_N = \frac{I}{k} \quad (A.7)$$

$$Soil_C = \frac{k(a_R r_P + a_H r_R)}{a_P a_R I} \quad (A.8)$$

$$Plant_N = -\frac{a_R q r_P + a_H q r_R + a_P r_H r_R \beta (\pi - \tau)}{a_P (a_R r_P \alpha (-1 + \delta) + a_H r_R \beta (-1 + \tau))} \quad (A.9)$$

$$Herbivore_N = \frac{r_R}{a_R} \quad (A.10)$$

$$Predator_N = -\frac{a_H a_R q r_P + a_H^2 q r_R + a_H a_P (-1 + \pi) r_H r_R \beta + a_P a_R r_H r_P \alpha (-1 + \delta)}{a_P a_R (a_R r_P \alpha (-1 + \delta) + a_H r_R \beta (-1 + \tau))} \quad (A.11)$$

where N stands for nitrogen and C stands for carbon. *S*, *P*, *H*, and *R* stand for soil, plants, herbivores, and predators, respectively. Parameters are briefly described in Table A.1, and a more detailed one in [12]. As in scenarios (1) and (2), plant, herbivore, and predator C content are recovered as,

$$Plant_C = \alpha \cdot Plant_N \quad (A.12)$$

$$Herbivore_C = \beta \cdot Herbivore_N \quad (A.13)$$

$$Predator_C = \beta \cdot Predator_N \quad (A.14)$$

A.2 Parameterizing the Model.

Before parameterizing the model, we transform the data sourced from the literature to shared units of measurements. Because we are interested in the influence of herbivores and predators on ecosystem carbon budgets, we seek to have the **processes** that shape ecosystem carbon capture (i.e., primary productivity and net ecosystem carbon balance) expressed as kg C m⁻² d⁻¹. Tables A.1 and A.2 show the empirical parameter values sourced from the literature after being transformed to common units of measurement, and Box 1.4 below offers details on these transformations. We assign these values to each parameter in the model to simulate the white-tailed deer-puma (Table A.1) and collared peccary-jaguar (Table A.2) food webs.

i Box 1.4: Details on unit transformations

The literature-sourced parameter values are variously expressed in units of:

- mass time⁻¹
- mass mass⁻¹
- mass area⁻¹ time⁻¹
- amount of substance area⁻¹ time⁻¹

In performing the transformations required to express them all in the same units, we use the following conversions:

Table B.1. Reference values for conversion between units of measurement.

From	To
1 ha	10000 m ²
1 year	365 days
1 month	30 days
1 day	86400 seconds
1 day	1440 minutes
1 kg	1000 grams
1 gram	1000 mg
1 mg	1000 µg
1 gram	1000000 µg
1 mol	1000000 µmol
1 mol CO ₂	44.01 g

We use the following conversion factors to transform amounts of CO₂ and CH₄ to amounts of C.

Table B.2. Conversion factors used to transform carbon dioxide and methane amounts to carbon amounts.

Conversion	Factor
CO ₂ to C	0.27
C to CO ₂	3.67
CH ₄ to C	0.75

Finally, we use the following conversion factors, derived from the literature-sourced data to account for the ecological stoichiometry of the trophic compartment in our system.

Table B.3. Conversion factors used in quantifying the stoichiometry of the model's trophic compartments.

Compartment	What	Factor
animal	body C	0.51
plant	biomass C	0.45
soil	N stock	0.002

Table A1. Parameter values used to simulate the White-tailed deer-Puma food web.

Description	Scenario	Value	Units	Source	Model parameter
Environmental rates					
N inorganic inputs	Shared	1.97×10^{-6}	kg N m ⁻² day ⁻¹	22,23	<i>I</i>
Soil C leaching rate (Trees)	No animals	3.2×10^{-3}	kg C m ⁻² day ⁻¹	36,37	<i>q_S</i>
Soil C leaching rate (Shrubs)	No animals	5.15×10^{-2}	kg C m ⁻² day ⁻¹	33	<i>q_S</i>
Soil C leaching rate (Shrub)	Herbivore	4.2×10^{-3}	kg C m ⁻² day ⁻¹	33	<i>q_S</i>
Soil C leaching rate (Shrub)	Herbivore-predator	2.1×10^{-2}	kg C m ⁻² day ⁻¹	33	<i>q_S</i>
Soil N leaching rate	Shared	4×10^{-8}	day ⁻¹	38	<i>k</i>
Uptake rates					
Plant (Tree) N uptake rate	No animals	1.58×10^{-2}	day ⁻¹	24	<i>a_P</i>
Plant (Shrub) N uptake rate	No animals	1.78×10^{-2}	day ⁻¹	24	<i>a_P</i>
Plant (Shrub) N uptake rate	Herbivore	1.78×10^{-3}	day ⁻¹	24	<i>a_P</i>
Plant (Shrub) N uptake rate	Herbivore-predator	7.6×10^{-3}	day ⁻¹	24	<i>a_P</i>
Herbivore (WTD) attack rate– Shrubs	Herbivore	0.84	kg C day ⁻¹	25,26	<i>a_H</i>
Herbivore (WTD) attack rate– Shrubs	Herbivore-predator	0.49	kg C day ⁻¹	25,26	<i>a_H</i>
Carnivore (Puma) attack rate	Herbivore-predator	9.15	kg C day ⁻¹	27	<i>a_R</i>
Respiration rates					
Plant (Tree) respiration rate	No animals	1.8×10^{-4}	kg C m ⁻² day ⁻¹	28	Contributes to δ
Plant (Shrub) respiration rate	No animals	1.8×10^{-4}	kg C m ⁻² day ⁻¹	28	Contributes to δ
Plant (Shrub) respiration rate	Herbivore	1.6×10^{-4}	kg C m ⁻² day ⁻¹	28	Contributes to δ
Plant (Shrub) respiration rate	Herbivore-predator	1.59×10^{-4}	kg C m ⁻² day ⁻¹	28	Contributes to δ
Herbivore (WTD) respiration rate	Herbivore	2.91×10^{-1}	kg C day ⁻¹	29,30	Contributes to π
Herbivore (WTD) respiration rate	Herbivore-predator	2.91×10^{-1}	kg C day ⁻¹	29,30	Contributes to π
Carnivore (Puma) respiration rate	Herbivore-predator	8.12×10^{-1}	kg C day ⁻¹	30	Contributes to τ
Recycling rates					
Plant (Tree) recycling (litterfall) rate	Shared-no subsidy	5.55×10^{-4}	kg C m ⁻² day ⁻¹	31,32,33	<i>r_P</i>
Plant (Tree) recycling (litterfall) rate	Shared-with subsidy	9.88×10^{-4}	kg C m ⁻² day ⁻¹	31,32,33	<i>r_P</i>
Plant (Shrub) recycling (litterfall) rate	No animals	4.71×10^{-4}	kg C m ⁻² day ⁻¹	33	<i>r_P</i>
Plant (Shrub) recycling (litterfall) rate	Herbivore	3.53×10^{-5}	kg C m ⁻² day ⁻¹	33	<i>r_P</i>
Plant (Shrub) recycling (litterfall) rate	Herbivore- predators	7.06×10^{-4}	kg C m ⁻² day ⁻¹	33	<i>r_P</i>
Herbivore (WTD) total recycling rate	Herbivore	4.96×10^{-1}	kg C day ⁻¹	34	<i>r_H</i>
Herbivore (WTD) total recycling rate	Herbivore-predator	4.25×10^{-2}	kg C day ⁻¹	35*	<i>r_H</i>
Carnivore (Puma) total recycling rate	Herbivore-predator	9.6×10^{-4}	kg C day ⁻¹	35	<i>r_R</i>
C:N ratios					
Plant (Trees) C:N ratio	Shared	75		16	α
Plant (Shrubs) C:N ratio	Shared	42		16	α
Animal C:N ratio	Shared	3.29			β

Table A2. Parameter values used to simulate the collared peccary-jaguar food web.

Description	Scenario	Value	Units	Source	Model parameter
N inorganic inputs	Shared	1.97×10^{-6}	kg N m ⁻² day ⁻¹	22,23	I
Soil C leaching rate (Trees)	Shared	3.2×10^{-3}	kg C m ⁻² day ⁻¹	36,37	q_S
Soil C leaching rate (Shrubs)	No animals	5.15×10^{-2}	kg C m ⁻² day ⁻¹	33	q_S
Soil C leaching rate (Shrub)	Herbivore	4.2×10^{-3}	kg C m ⁻² day ⁻¹	33	q_S
Soil C leaching rate (Shrub)	Herbivore-predator	2.1×10^{-2}	kg C m ⁻² day ⁻¹	33	q_S
Soil N leaching rate	Shared	4×10^{-8}	day ⁻¹	38	k
Uptake rates					
Plant (Tree) N uptake rate	Shared	1.58×10^{-2}	day ⁻¹	24	a_P
Plant (Shrub) N uptake rate	No animals	1.78×10^{-2}	day ⁻¹	24	a_P
Plant (Shrub) N uptake rate	Herbivore	3.56×10^{-3}	day ⁻¹	24	a_P
Plant (Shrub) N uptake rate	Herbivore-predator	2.22×10^{-3}	day ⁻¹	24	a_P
Herbivore (Peccary) attack rate-Shrubs	Herbivore	0.24	kg C day ⁻¹	44	a_H
Herbivore (Peccary) attack rate-Shrubs	Herbivore-predator	0.13	kg C day ⁻¹	44	a_H
Carnivore (Jaguar) attack rate	Herbivore-predator	4.35	kg C day ⁻¹	45	a_R
Respiration rates					
Plant (Tree) respiration rate	Shared	1.8×10^{-4}	kg C m ⁻² day ⁻¹	28	Contributes to δ
Plant (Shrub) respiration rate	No animals	1.8×10^{-4}	kg C m ⁻² day ⁻¹	28	Contributes to δ
Plant (Shrub) respiration rate	Herbivore	1.6×10^{-4}	kg C m ⁻² day ⁻¹	28	Contributes to δ
Plant (Shrub) respiration rate	Herbivore-predator	1.2×10^{-4}	kg C m ⁻² day ⁻¹	28	Contributes to δ
Herbivore (Peccary) respiration rate	Herbivore	9.34×10^{-2}	kg C day ⁻¹	30,46	Contributes to π assumes 1.5 x BMR from 46,47
Herbivore (Peccary) respiration rate	Herbivore-predator	9.34×10^{-2}	kg C day ⁻¹	30,46	Contributes to π assumes 1.5 x BMR from 46,47
Carnivore (Jaguar) respiration rate	Herbivore-predator	4.77×10^{-1}	kg C day ⁻¹	30	Contributes to τ assumes 3x BMR
Recycling rates					
Plant (Tree) recycling (litterfall) rate	Shared-no subsidy	5.55×10^{-4}	kg C m ⁻² day ⁻¹	31,32,33	r_P
Plant (Tree) recycling (litterfall) rate	Shared-with subsidy	9.88×10^{-4}	kg C m ⁻² day ⁻¹	31,32,33	r_P
Plant (Shrub) recycling (litterfall) rate	No animals	4.71×10^{-4}	kg C m ⁻² day ⁻¹	33	r_P
Plant (Shrub) recycling (litterfall) rate	Herbivore	3.53×10^{-5}	kg C m ⁻² day ⁻¹	33	r_P
Plant (Shrub) recycling (litterfall) rate	Herbivore-predators	7.06×10^{-4}	kg C m ⁻² day ⁻¹	33	r_P
Herbivore (Peccary) total recycling rate	Herbivore	4.03×10^{-1}	kg C day ⁻¹	35,47	r_H
Herbivore (Peccary) total recycling rate	Herbivore-predator	3.45×10^{-2}	kg C day ⁻¹	35,47	r_H
Carnivore (Jaguar) total recycling rate	Herbivore-predator	1.36×10^{-4}	kg C day ⁻¹	35,48	r_R
C:N ratios					
Plant (Trees) C:N ratio	Shared	75		16	α
Plant (Shrubs) C:N ratio	Shared	42		16	α
Animal C:N ratio	Shared	3.29			β

As Tables A.1-A.2 show, some parameter values are shared across modeling scenarios, whereas others change—e.g., the values for plant respiration and recycling rates, or the soil C leaching rate. Respiration loss data for both plants and herbivores enter the model as **proportions of C lost** from their trophic compartment through respiration, with the remaining part (i.e., $1-\delta$, $1-\pi$, $1-\tau$) being recycled in the soil compartment. Data from the literature, however, rarely capture auto- or hetero-trophic respiration as a proportion of C lost. Hence, before running the model, we transformed these data to proportions. For plants, the proportion of C lost through respiration (δ) is,

$$\frac{\text{plant respiration rate}}{\text{plant respiration rate} + \text{plant recycling rate } (r_p)} \quad (\text{A. 15})$$

When the model comprises animals, the proportion of C they respire (π for herbivores, τ for predators) is,

$$\frac{\text{animal respiration rate}}{\text{animal respiration rate} + \text{animal recycling rate } (r_i)} \quad (\text{A. 16})$$

Where $i \in [H, R]$. We calculate the proportional values of δ , π , and τ before running the model for any scenario.

A.3 Net Ecosystem Carbon Balance Calculations.

Net Ecosystem Carbon Balance (NECB) measures ecosystem carbon storage in terms of the net difference between an ecosystem's anabolic and catabolic processes, i.e., the balance between net rate of carbon accumulation in ecosystems due to carbon fixation by plants (primary productivity), heterotrophic (i.e., animals, microbes) production and respiration, as well as additional losses including CH emissions directly from animals and soils and sediments of ecosystems.^{1,2} Traditionally, net ecosystem carbon balance is estimated as:

$$NECB = \text{Gross Primary Production} - \text{Ecosystem Respiration} - \text{Lateral Fluxes} \quad (\text{A. 17})$$

Where Gross Primary Production is essentially gross carbon uptake by plants, Ecosystem Respiration comprises respiration by all trophic compartments (e.g., soil, plants, herbivores, predators³¹), and Lateral Fluxes comprise losses of C through mechanisms other than respiration (e.g., leaching to groundwater, methane emissions). However, by only accounting for the effects of heterotrophs through respiration, equation A.17 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 A.17 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,

$$NECB = NPP + NHP \quad (\text{A. 18})$$

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 (i.e., plants) compartment of an ecosystem. If we imagine a terrestrial ecosystem, where primary producers are generally plants, we can then specify:

$$NPP = \text{Gross Plant Production} - \text{Plant Respiration} \quad (\text{A. 19})$$

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 (i) any trophic level above the autotrophs—e.g., herbivores, predators—but also (ii) 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, (i) comprises herbivores and predators, and (ii) is the soil. So, we obtain:¹²

$$\begin{aligned} NHP = & (\text{Predator Gross Production} - \text{Predator Respiration}) + \\ & (\text{Herbivore Gross Production} - \text{Herbivore Respiration}) + \\ & (\text{Soil Gross Production} - \text{Soil Respiration}) \end{aligned} \quad (\text{A. 20})$$

Where Gross Production is measured as the C uptake rate by a given trophic compartment. Equation A.20 is conceptually comparable to equation A.17 but allows for debiting heterotrophic respiration from heterotrophic production. Accounting for both components of heterotrophic C effects allows us to explicitly measure the relative impact of different kinds of heterotrophs on NECB. Thus, for the soil-plant (S-P) equilibrium of scenario (1), NECB is calculated as,

$$NECB_{S-P} = \frac{q_S r_P}{a_P} \quad (\text{A. 21})$$

And, for the soil-plant-herbivore (S-P-H) equilibrium of scenario (2), NECB is,

$$NECB_{S-P-H} = - \frac{r_H r_P \alpha (a_P r_H (\alpha + (-1 + \pi) \beta) (-1 + \delta) + a_H q_S \delta)}{a_H (a_H q_S + a_P (-1 + \pi) r_H \beta)} \quad (\text{A. 22})$$

Finally, for the soil-plant-herbivore-predator (S-P-H-R) equilibrium of scenario (3), NECB is,

$$NECB_{S-P-H-R} = \frac{a_R r_P r_R (a_H q_S (\alpha (\delta - 2) + \beta (\tau - 2)) - \alpha a_P \beta (\delta - 1) r_H) + a_H r_R^2 (a_P \beta r_H (\alpha \tau + \beta - \pi (\alpha + \beta)) - a_H q_S (\alpha - \beta \tau + 2 \beta)) + \alpha a_R^2 (\delta - 1) q_S r_P^2}{a_P a_R (a_H \beta r_R (\tau - 1) + \alpha a_R (\delta - 1) r_P)} \quad (\text{A. 23})$$

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