

Mammal diversity influences the carbon cycle through trophic interactions in the Amazon

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Biodiversity affects many ecosystem functions and services, including carbon cycling and retention. While it is known that the efficiency of carbon capture and biomass production by ecological communities increases with species diversity, the role of vertebrate animals in the carbon cycle remains undocumented. Here, we use an extensive dataset collected in a high-diversity Amazonian system to parse out the relationship between animal and plant species richness, feeding interactions, tree biomass and carbon concentrations in soil. Mammal and tree species richness is positively related to tree biomass and carbon concentration in soil—and the relationship is mediated by organic remains produced by vertebrate feeding events. Our research advances knowledge of the links between biodiversity and carbon cycling and storage, supporting the view that whole community complexity—including vertebrate richness and trophic interactions—drives ecosystem function in tropical systems. Securing animal and plant diversity while protecting landscape integrity will contribute to soil nutrient content and carbon retention in the biosphere.

Biodiversity is expected to affect the ability of forests to sequester carbon dioxide from the atmosphere¹. This is due to both the increased likelihood of highly productive species being present² and a rise in the use of limiting resources due to complementarity effects³. Plant diversity increases biomass production (carbon sequestration) and soil organic matter^{4–7}. After biomass is formed, it can be consumed by herbivores or die. After death, organic litter can be decomposed or stored as organic matter. Thus, diversity of the whole community, including animals, may influence carbon concentration in soil, which might eventually impact carbon stored in tree biomass⁸. However, the relationship between mammal diversity and carbon cycle components in tropical forests remains undocumented.

Because multiple processes and trophic levels influence the flows and equilibrium levels of carbon in soil and biomass, the relationship between biodiversity and carbon cycling is challenging to resolve. The microbial and soil invertebrate communities that are at the centre of decomposition and mineralization processes, and the plant material that is the primary input to soil organic matter are the most studied and best understood biotic contributors to soil carbon. Relationships between measures of diversity and carbon are documented for plant diversity^{4–7,9} and soil microbe and invertebrate diversity^{10,11}. Despite strong evidence for vertebrate diversity–carbon relations in aquatic systems¹², such evidence is lacking in terrestrial systems—although models show a potential relationship between mammals and biomass through seed-dispersal influences on plant community composition¹³.

At local scales, vertebrate populations impose important variation on soil organic matter. Carcasses and waste products have significant impact on local soil nutrient composition^{14–17}, which cascades down to the microbial community and its nutrient metabolism^{10,18}. Dead biomass is part of the natural carbon cycle. When decomposed, it releases carbon as carbon dioxide or is converted to increasingly longer-term stores of primarily microbial-derived

compounds¹⁹, which decelerates release of carbon into the atmosphere. Models and experimental evidence in grassland systems demonstrate that mammal herbivory affects carbon in soil^{20–22}, with the direction of the effect depending on the intensity of herbivore pressures²¹ or plant community composition²².

Considering these documented impacts of individual species or functional groups, we asked whether mammal species richness is linked to carbon concentration in soil and tree biomass in a hyperdiverse tropical system at a landscape scale (Fig. 1). To answer this question, we gathered a rich dataset on mammal and tree species richness (Supplementary Table 1), carbon concentration in soil, tree biomass and environmental variables across 4,800,000 ha in the Rupununi region of Guyana, a mixed forest–savanna landscape occupied primarily by indigenous communities at low population densities. The predominant livelihood in the area is subsistence hunting, fishing and farming. No large-scale habitat degradation exists in the study area, though a few villages practice small-scale selective timber extraction for local use.

Mammal occurrence was recorded biweekly through sign and sightings on 215 transects of 4 km in length during 3 years (a total of 10,027 animal surveys, with 49 ± 15 s.d. surveys per transect; Fig. 1). A total of 218,163 individual mammals belonging to 48 spp. were identified (Supplementary Table 1). In addition, 43,448 feeding events (carnivorous, herbivorous or frugivorous interactions) and 1,004,876 remains on the ground (animal parts, faeces, vegetative parts, and fruits and seeds previously handled by animals) were also recorded. All feeding events recorded were direct observations of animals feeding, whether on other animals, on plant parts or on fruits. Soil carbon concentrations were measured as percent carbon content in 825 samples along 121 of these transects. Tree carbon was measured as biomass in 120 transects where 46,871 trees were measured (diameter at breast height (DBH)) and identified.

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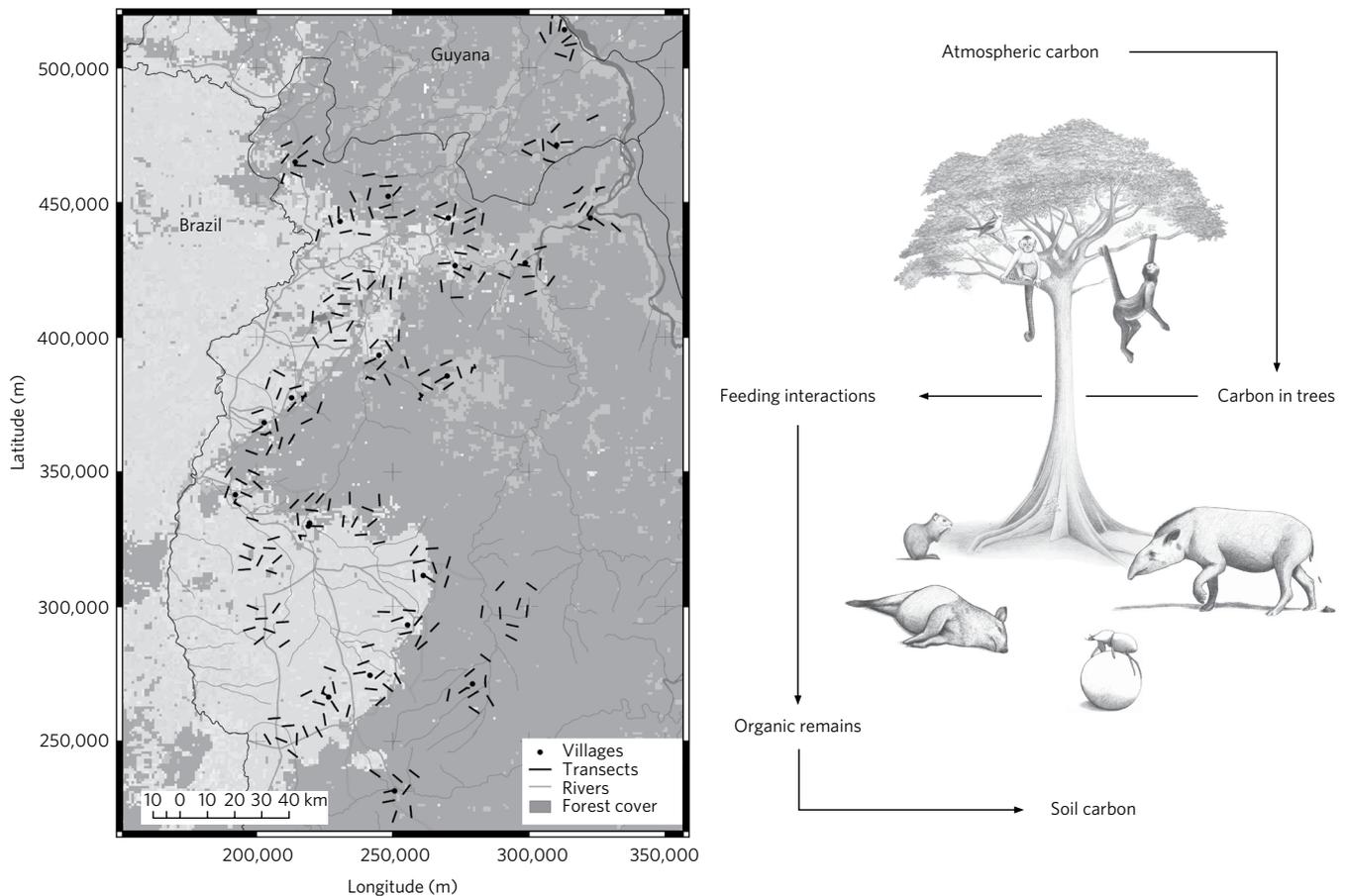


Fig. 1 | Map of the study area in Guyana (WGS 84/UTM zone 21N; short lines indicate surveyed transects) and diagram of hypothesized ecological interactions that link atmospheric, biotic and soil carbon pools. This diagram does not show major carbon pathways such as litterfall.

We used generalized linear mixed models (GLMMs) and structural equation models (SEMs) to investigate the relationship between mammal species richness and both woody biomass and soil carbon concentration. Species richness is a primary component of diversity pertinent to the study of ecosystem services at broad geographical ranges¹². Because richness was estimated at the transect level, all the other variables were aggregated at the transect level. Transects were arranged in a stratified random manner resulting in spatial clustering in 27 different transect arrays. Spatial arrangement of transects was controlled for by adding the transect array as a random factor in the statistical models. Because underlying, spatially patterned environmental variation could independently drive trends in both richness and carbon, our models additionally accounted for environmental variation: geographical location, temperature, precipitation and distance to nearest river, road and village were included as covariates to control for their effects.

Results

Latitude was the variable that most influenced carbon concentration in soil and carbon per tree, while precipitation most influenced carbon per area. Tree biomass and carbon concentration in soil were higher towards the north of the study area, which may be due to other environmental gradients, potentially related to latitude, such as geologic composition. In addition, precipitation and temperature negatively affected biomass carbon (Table 1). Carbon concentration in soil increased with distance from roads, and carbon in trees increased with distance from villages (Table 1). This might be explained by border effects related to habitat fragmentation and/or

increased human impacts along roads and near villages, such as gathering of timber and non-timber products.

Mammal and tree richness explained variation in soil carbon and carbon in biomass, in addition to that explained by environmental factors (Table 1 and Fig. 2). The effects of mammal and tree richness on carbon in soil were similarly important (see coefficient estimates in Table 1). Neither carbon per tree nor per area were significant explanatory variables of carbon concentration in soil (thus they were not included in the final models), which indicates that in our system, tree biomass does not directly impact carbon concentration in soil (when controlling for tree and mammal richness and environmental variation). Adding mammal abundance as a predictor variable was not significant either and its effect did not improve the fit of our models. The lack of effect of both tree biomass and animal abundance on the response variables highlights the relevance of species richness. In addition, mammal and tree richness were themselves explained by environmental variation and therefore were correlated with each other (Supplementary Table 2 and Supplementary Fig. 1).

The positive relationship of mammal and tree species richness with biomass and carbon concentration in soil may occur if complementarity, facilitation and insurance effects increase the community-level use of limiting resources²³. However, we wished to move beyond these general explanatory frameworks and explore potential mechanistic linkages between mammals and carbon. Animal bodies, faeces and fruits processed by animals are available to become soil organic matter along with litter directly produced by plants. Using a SEM, we found that

Table 1 | Results of generalized linear mixed models performed to explain carbon concentrations in soil and carbon in biomass

		Variance	s.d.	Estimate	s.e.	d.f.	t-value	P-value
Carbon in soil (%)	Mammal richness			0.176	0.0824	107	2.143	0.034
	Tree richness			0.184	0.0825	106	2.240	0.027
	Distance nearest road			0.272	0.103	44	2.646	0.011
	Distance nearest river			0.123	0.085	108	1.444	0.151
	Distance nearest village			0.037	0.071	107	0.522	0.602
	Longitude			−0.230	0.144	67	−1.597	0.115
	Latitude			0.328	0.105	38	3.117	0.003
	Temperature			−0.013	0.083	73	−0.161	0.872
	Precipitation			−0.141	0.106	35	−1.331	0.192
	Transect array (random)	0.0421	0.205					
$R^2_m = 0.322$								
$R^2_c = 0.374$								
Carbon per tree (kg)	Mammal richness			52.681	19.787	121	2.662	0.009
	Tree richness			28.468	18.933	121	1.504	0.135
	Distance nearest road			22.160	30.319	92	0.731	0.467
	Distance nearest river			−4.146	17.172	109	−0.241	0.809
	Distance nearest village			33.980	15.198	112	2.236	0.027
	Longitude			−38.946	38.612	93	−1.009	0.315
	Latitude			66.972	31.671	39	2.115	0.041
	Temperature			−38.866	22.589	120	−1.721	0.087
	Precipitation			−16.977	35.808	46	−0.474	0.638
	Transect array (random)	22709	150.7					
$R^2_m = 0.225$								
$R^2_c = 0.622$								
Carbon per area (Mg ha^{−1})	Mammal richness			−9.821	8.029	697	−1.223	0.222
	Tree richness			16.310	7.665	577	2.128	0.034
	Distance nearest road			−4.985	11.444	78	−0.436	0.664
	Distance nearest river			2.127	7.106	3857	0.299	0.765
	Distance nearest village			5.521	6.263	2418	0.882	0.378
	Longitude			8.812	14.621	87	0.603	0.548
	Latitude			27.218	11.100	30	2.452	0.020
	Temperature			3.088	8.833	163	0.350	0.727
	Precipitation			−32.709	12.766	37	−2.562	0.015
	Transect array (random)	2×10^9	45,052					

Note that 125 transects were included in the analyses of carbon per tree and tree carbon per area, while 111 transects were included in the analyses of carbon concentration in soil. Explanatory variables were all centred and standardized (subtracted the mean and divided by their standard deviation) so effects sizes among explanatory variables are comparable among them (within each model). Marginal and conditional coefficients of multiple determination (R^2) are shown (R^2_m and R^2_c), which respectively explain the amount of variation in the response variable explained by fixed factors alone or by the whole model.

mammal richness (which in our system comprises herbivores (including frugivores, granivores and browsers), omnivores, and primary and secondary carnivores) influences carbon concentration in soil—and ultimately carbon in biomass—through the organic remains produced by feeding interactions (Fig. 3). We eliminated alternative hypotheses whereby carbon per tree or per area are relevant to carbon concentration in soil, soil carbon drives mammal richness, or trophic interactions are not relevant to organic remains (see alternative models in Supplementary Figs. 2 and 3). The solution to the best model fit revealed that mammal and tree richness increase the number of feeding interactions observed. The amount of organic remains (fruit and seed parts, non-fruit plant parts, faeces and animal parts) on the ground is predicted by the number of feeding interactions, and is positively related to carbon concentration in the soil. The organic remains that most affect soil carbon concentration were animal and fruit remains, which were themselves driven by carnivory and frugivory interactions (Supplementary Tables 3 and 4) suggesting that both processing of fruits and direct biomass contributions by vertebrates and plants affect soil carbon concentration (Fig. 3).

Discussion

Large-bodied seed dispersers such as tapirs, peccaries and primates ingest, digest and defecate large amounts of fruit pulp and seeds, as well as grasses and leaves^{24,25}, moving plant matter across the landscape and processing it in ways that make it available to a larger diversity of invertebrates, fungi and microbes. Plant and food matter moved by these animals is secondarily buried by dung beetles²⁶, by scatterhoarding rodents, or through trampling and rooting by ungulates. Defaunation studies have documented that variation in animal abundance and diversity impacts fruit and seed consumption^{27,28}. The diversity of all vertebrates, including herbivores, carnivores, omnivores and insectivores, will influence the amount and nutrient composition of plant and animal biomass that enters the soil. The amount and composition of animal biomass and processed and unprocessed plant parts will influence the activity of microbes and the decomposition, mineralization or retention of carbon in soil (Figs. 1 and 3). We documented a relationship between mammal and tree species richness and carbon concentration in soil and carbon stored in tree biomass, and identified biotic interactions as

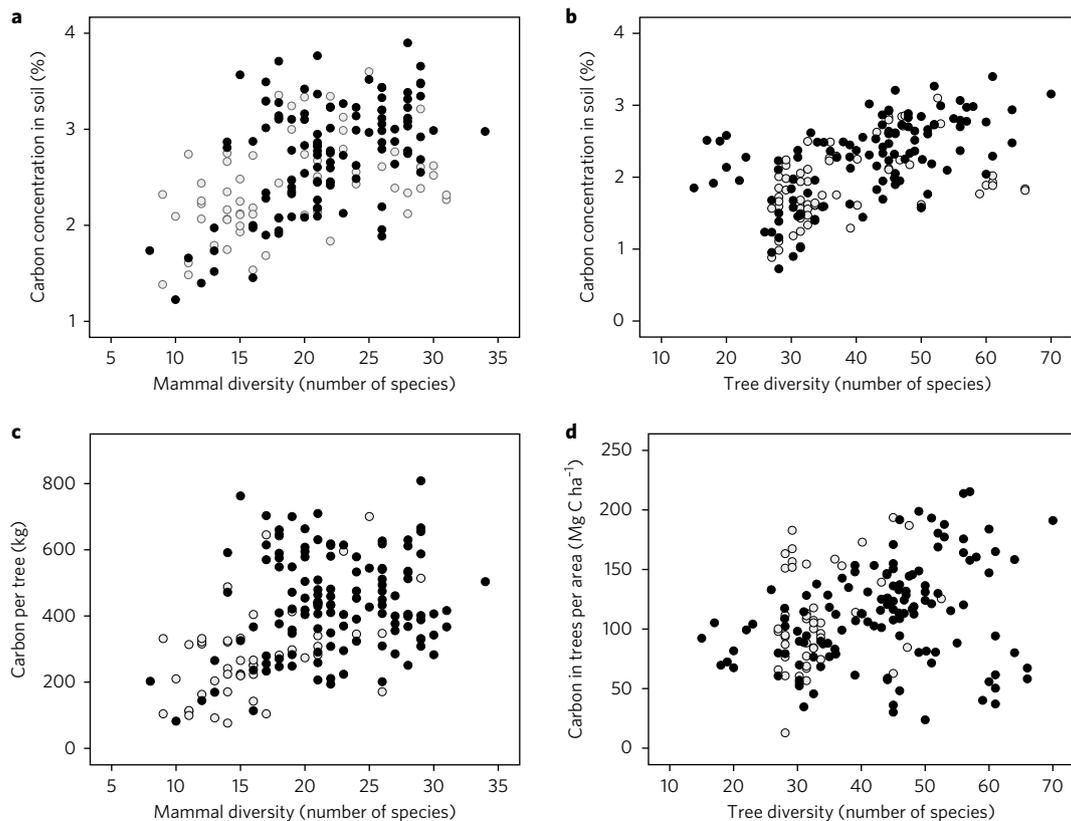


Fig. 2 | Results of the richness-carbon relationships. **a**, Mammal diversity and carbon concentration in soil. **b**, Tree diversity and carbon concentration in soil. **c**, Mammal diversity and carbon stored per tree. **d**, Tree diversity and carbon in trees stored per area. Number of species of trees and mammals per transect are shown. Black dots represent transects for which we had data for the response variables (111 in the case of carbon concentration in soil and 125 in the case of tree carbon). White dots represent the values estimated by models from observed richness data on the remaining 48 transects with data for all predictor variables.

one possible mechanism underpinning the relationship. In addition, our results show that mammal richness may also have an indirect influence on aboveground carbon through the positive relationship between carbon in soil and biomass carbon per tree and per area (Fig. 3).

Other components of diversity, such as functional diversity, may also influence ecosystem function²⁹. In at least one aquatic system, however, species richness emerges as the key measure of biodiversity related to carbon levels at landscape scales, with a stronger impact than functional diversity¹². Additional study is needed in our system to understand the role of key functional groups, such as soil disturbers (armadillos, peccaries), large-bodied herbivores (tapirs, deer), scatterhoarding rodents (agoutis, squirrels, small rodents) and arboreal species, among others. As predicted by previous work³⁰, the relationship between biodiversity, ecosystem function and ecosystem services depends on multiple, interacting ecological functions mediated at multiple trophic levels, and cannot be easily deconstructed into individual function-service relationships. Much work remains to be done to parse out the multiple mechanisms by which mammalian diversity might influence nutrient cycling in highly diverse tropical systems.

Our study documents with empirical data that mammal richness plays a role in the carbon cycle in the Amazon—even after controlling for environmental effects and the effect of tree richness. Latitude, precipitation and spatial distribution of transects (see conditional R^2 compared with marginal R^2 in biomass carbon models, Table 1) have additional important effects in the carbon cycle components in our system.

Conclusion

Our results suggest that management of vertebrate diversity may provide carbon-retention benefits that are additive to those provided by forest cover protection. By sustainably managing and protecting vertebrate diversity, humanity may help secure services provided by nature, such as the production of food, fibre or timber, and the retention of carbon in the biosphere.

Methods

The study was conducted in the Rupununi region of Guyana (Fig. 1) in the Northern Amazon. The area comprises around 4,800,000 ha of moist tropical forest and savanna, an area about the size of Costa Rica, inhabited predominantly by Makushi and Wapishana indigenous people. Village population size varies from 122 to 1,192 people. The indigenous communities remain largely isolated due to their remoteness from Guyanese population centres on coastal areas, to which they are poorly connected by an inadequately maintained dirt road^{31–35}.

In this area, 215 4-km-long transects were placed in a stratified random manner (separated at least 3 km from each other, Fig. 1) and were sampled in the context of a socio-environmental study^{31–35}. Transects were placed in 27 different transect arrays (of 8 transects each, but one with 7). Within arrays, transects were randomly placed at between 6 and 12 km of a central point. Transect array identity was later controlled for in analyses. The savanna-forest transition and highland-lowland gradients that characterize the study area created important among-transect environmental variation. At the meso- or landscape scale of our study, biodiversity is probably influenced by elevation differences, flood regimes and moisture gradients. The signature of macroscale processes, such as palaeoclimatic changes and macrogeologic disturbance is unlikely to be detected at this scale. For each transect, local characteristics—longitude, latitude, aspect, slope, elevation, precipitation, temperature (precipitation and temperature extracted from ref. ³⁶), distance to nearest river, distance to nearest road (only unimproved single-lane and one improved two-lane dirt roads exist in the area) and distance to

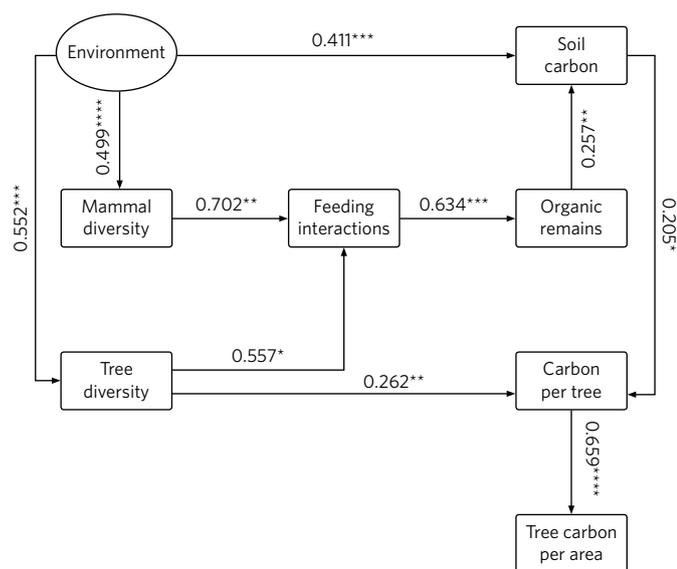


Fig. 3 | Results of the structural equation model analysing the relationship of mammal richness, tree richness, feeding interactions and organic remains with carbon concentration in soil, carbon per tree and tree carbon per area. We show coefficients for each significant path.

* $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$, **** $P < 0.001$. $n = 106$ transects. Note that environment is a latent variable in this model and that the direct relationship between tree richness and tree carbon per area, as well as the effect of environment on feeding interactions, organic remains and carbon per tree, were also included in the model and were not significant. Initial model and other alternative models with and without solutions can be found in Supplementary Figs. 2 and 3.

nearest village—were described to control for environmental variation that might influence carbon cycle components. Animal and tree censuses were performed by technicians from 23 Amerindian communities within the area, who were trained specifically for this study. Three- (carbon) and five- (animal and tree richness) day classroom and field training sessions were held in three locations³³.

Mammal richness. Methodology was selected to optimize mammal richness records (using standard distance sampling methods³⁷). Volant mammals and small terrestrial mammals were not sampled. Mammal occurrence was quantified on all 215 transects. From May 2007 to June 2010, independent biweekly surveys were conducted on each transect—once a month for animal signs (tracks, burrows and so on) detected in a 1-m-wide strip, and once a month for direct animal encounter data. Each of the 215 transects was walked an average of 49 times (s.d. = 15). The number of transects walked during the study was sufficient for the abundance data per species to reach an asymptote with at least one of the methods (signs or signs); an in-depth study of this issue in the same transects³⁵ showed that 32 vertebrate species were detected either by sign or sighting method within the first five surveys along transects. Our approach is therefore very conservative, as survey numbers were much greater than the minimum 5 surveys per transect (49 ± 15 surveys per transect) and obtained a reliable estimate of mammal richness along the different transects. This dataset (drawn from a total of 10,027 animal surveys) includes direct encounters of 132,995 individuals and sign records of 190,369 individuals for 218 animal species (48 mammal species, 144 bird species, 21 reptile species and 6 amphibian species). Because our methodology was designed to optimize mammal richness estimations, we used only mammal richness data in this work (Supplementary Table 1). Mammal richness was assessed by combining data from both the direct encounter and the sign datasets. Because direct encounter data and sign data provide different information depending on the ecology of the species (for example, nocturnal versus diurnal, terrestrial versus arboreal and so on), the most complete assessment of richness is achieved by combining both data types³⁵.

Tree richness. Tree species were identified (for all individuals with DBH > 25 cm) on 88 (10 m wide) transects during the period July–December 2008. This dataset included 46,871 individual trees from 206 taxa. Note that 53% were identified only to the genus level (Supplementary Table 1). Fruits and seeds on the ground were also identified (140 taxa) on the 215 transects once a month from May 2007 to June 2010 along a 1-m-wide strip. For 42 out of 130 transects used in the carbon analyses, we assessed tree richness using the very tight relationship between fruit

and tree richness (analysed for the 88 transects with both data types). The model that best explained tree richness was a generalized model fitted to a Poisson error distribution with a log link function; the only predictor variable was fruit richness both in its linear and quadratic form.

Ecological interactions and organic remains. A total of 43,448 feeding events were recorded. All feeding events recorded were direct observations of animals feeding on other animals, on plant parts or on fruits. Of those, 2,202 were herbivorous interactions (191 animals eating flowers, 840 eating grass, 929 eating leaves and 242 eating roots), 20,734 were granivorous or frugivorous interactions (4,610 animals eating seeds, 16,124 eating fruits) and 20,512 were carnivorous interactions (19,366 animals feeding on invertebrates and 1,146 feeding on vertebrates). Organic remains found on the ground were also recorded; 1,624 were animal parts (such as hairs, bones or entire carcasses), 2,016 were faeces and 470 were non-reproductive plant parts that had been handled by an animal (such as leaves, wood or bark). In addition, 793,907 fruits and 206,859 seeds previously handled by animals were recorded. Interactions and faeces/remains were recorded on all 215 transects. Note that ecological interactions and organic remains are simply abundance data and do not incorporate the mass of different types of remains. Data were later aggregated per transect as the total number of interactions (or organic remains) recorded by kilometre surveyed (depending on how many surveys were completed per transect).

Carbon in biomass. Aboveground biomass is a widely accepted surrogate for aboveground carbon stocks in ecosystems (see relevant references in ref. ¹). We investigated the relationship of animal and tree species richness with both the mean biomass (carbon) per individual tree and the carbon biomass per unit area.

To quantify tree biomass on all transects, we measured biomass at the individual tree level to obtain a measure of biomass not directly linked to forest cover. To estimate average carbon stored per tree, the DBH of all trees > 25 cm DBH along 120 transects was measured. All tree individuals were measured on 88 (10 m wide) transects and within 605 (0.01 ha) plots across 111 transects (1 to 8 plots per transect; average = 5, s.d. = 2). These data include 46,871 individual trees. Based on the regional rainfall regime, the allometric equation for moist tropical forests was used to calculate biomass and later multiplied by 0.5 to derive carbon³⁸.

$$Y = 0.5 - \exp\{-2.289 + 2.649 - \ln(\text{DBH}) - 0.021 - (\ln(\text{DBH}))^2\}$$

where Y expresses kg C per tree.

Thus, the carbon per tree at the transect level was the sum of the individual carbon per tree in each transect divided by the total number of trees measured in the transect. We assessed tree biomass per area (Mg C ha^{-1}) by multiplying the density of tree individuals per ha by the estimated carbon per tree within each transect.

Soil carbon concentration. Carbon concentration in soil was measured in 825 soil samples (sampling avoided animal latrines) from 121 transects at several points per transect (3 to 8 plots per transect; average = 6, s.d. = 2). Soil carbon data derived from measurements at a single point in time and were taken in the same period. Soil pits measured 20 cm in diameter. The forest floor was always removed and sampling started at first soil horizon. Oven-dried (110 °C) soil from the top 10 cm of each pit were sieved < 2 mm, and ground in an agate mortar and pestle. Although soil carbon is stored up to 200 cm depth³⁹, published soil carbon data generally derive from soil samples to 30 cm depth^{40,41}. In our study, the carbon content of 30 samples taken at 10–20 and 20–30 cm depths was strongly correlated with carbon content in the corresponding top 10 cm samples (correlation coefficient 0.720, $P < 0.01$, R^2 0.52).

Samples were weighed to +0.0005 mg on a Mettler Toledo microbalance in tin cups (Costech, 5 × 9 mm) and combusted in a Carlo Erba NA-1500 elemental analyser. Standard curves for carbon were generated using pre-weighed, authentic atropine, a plant-derived alkaloid (Costech), as a standard. Final data per sample was the average of three independent analyses, thus ($825 \times 3 = 2,475$ carbon analyses in soil were run). Soil carbon concentration per transect was assessed as the average value of carbon concentration in soil samples within each transect.

Statistical analyses. Richness and several predictor variables were observed at the transect level, therefore response variables were aggregated at the transect level. To control for potential spatial autocorrelation among transects within an array, transect array was included as a random factor in the models.

Generalized linear mixed models included environmental covariates with the purpose of controlling for concomitant environmental variation. Environmental variables included were precipitation, temperature, distance to the nearest road, distance to the nearest river, distance to the nearest village, latitude and longitude. Variables such as elevation, slope or nitrogen concentration (correlated with a Pearson's $r = 0.926$ with carbon concentration) were excluded to avoid collinearity issues. Final models (Table 1) included variables that either explained the response variable or improved the model fit for at least one of the response variables⁴².

The soil carbon–richness relationship was analysed using a GLMM in which percent of carbon in soil (at the transect level) was the response variable. Predictor variables included the corresponding environmental variables and mammal and tree richness (and transect array as a random factor). This model was fit by means of a normal error distribution and an identity link function. This model was also run including carbon per tree, carbon per area and mammal abundance as predictor variables. None of those variables predicted carbon concentration in soil and did not improve model fit.

The tree carbon–richness relationship was analysed using a GLMM in which average carbon stored per tree (at the transect level) was the response variable. Predictor variables included the corresponding environmental variables and mammal and tree richness (and transect array as a random factor). This model was fit by means of a normal error distribution and an identity link function. We also analysed nitrogen in soil in 85 transects, to determine whether the relationship between tree richness and carbon in biomass was mediated by soil nutrients. Inclusion of nitrogen as a covariate to explain carbon in biomass was not significant, and the relationship between plant richness and biomass carbon remained unchanged. Nitrogen does not seem to underlie the relationship between tree richness and tree carbon in this study. The nitrogen effect was not included in the models because the results remained the same and nitrogen data were available for only 85 transects, which would have reduced the sample size from 125 transects to 85 transects.

The tree carbon per area–richness relationship was analysed by a GLMM in which tree carbon per area (at the transect level) was the response variable. Predictor variables included the corresponding environmental variables and mammal and tree richness (and transect array as a random factor). This model was fit by means of a normal error distribution and an identity link function.

We performed equivalent analyses for the subset of transects located completely within forests for all the response variables and results remained the same.

Mammal abundance (as the average number of recorded mammals per walked kilometre in each transect) was additionally included as a predictor in all the models and did not explain or improve the data fit for any of the response variables.

Additionally, the effects of different types of organic remains on the concentration of carbon in soil and the effects that different types of ecological interactions have on organic remains were analysed by a GLMM fitted to a normal error distribution and including transect array as a random factor with the environmental covariates included for control.

Explanatory variables were standardized (by subtracting the average and dividing by their standard deviation) to get comparable slope values. Computations were performed in open source R environment version 2.15.1 (ref.⁴³).

A simultaneous analysis of all relationships was performed to find support for possible mechanistic hypotheses of links between mammal richness and carbon stored in soil. We analysed the relationships between tree richness, mammal richness and carbon, considering the feeding interactions and organic remains on the ground. We performed a SEM in which we included the following manifest variables at the transect level⁴⁴: mammal richness, tree richness, number of feeding interactions, abundance of organic remains on the ground, percentage of carbon in soil, carbon stored per tree and tree carbon per unit area. As a latent variable⁴² we included environment. Note that a latent variable in SEM models is not observed, it is a construct of the model based on the variables that it predicts⁴²; thus, environment in the SEM model does not include the observed environmental variables included in the GLMMs. We had 106 transects with information available for all these covariables; therefore, our data could be used for structural models with up to 20 parameter estimations⁴⁴, which enables us to properly test our mechanistic hypothesis. For the SEM analyses, all variables were transformed for normality and standardized so we have parameter estimates based on standardized variables. We tested models based on our knowledge of the system. Different models (see Supplementary Figs. 2 and 3 for some examples) were analysed and from this standpoint model selection was made⁴⁴; we tested the goodness of fit of the models by means of maximum-likelihood estimation on the variance–covariance matrix. The chi-squared *P*-value of the chosen solution was 0.411 (X^2 statistic, 6.112; d.f., 6; a non-significant goodness of fit test indicates that the model is a good description of the observed covariance among the variables⁴⁴). We used the generalized least squares shifting to maximum-likelihood method to calculate the covariation parameters. Structural equation modelling was performed with SEPATH procedure in Statistica (StatSoft)⁴⁵.

Data availability. Due to human rights concerns and respect for intellectual property right, an agreement exists between the principal investigator (J.M.V.F.) and the indigenous communities in Guyana that participated in this study that no data can be posted that could identify either communities or individuals. Those interested in the data should contact J.M.V.F. at fragoso@stanford.edu to determine whether the data can be made available on a case-by-case basis without identifiers.

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Author contributions

J.M.V.F., M.S., K.M.S. and L.F.B.O. conceptualized this study. M.S. completed the statistical analyses. J.M.V.F., K.M.S., H.O., L.F.B.O., T.K.R. and other colleagues designed the field study and/or oversaw data collection. M.S. and K.M.S. drafted the manuscript with all authors participating in revisions.

Competing interests

The authors declare no competing financial interests.

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