SHORT COMMUNICATION

Green sloths and brown cows: the role of dominant mammalian herbivores in carbon emissions for tropical agro-ecosystems

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ABSTRACT

When Neotropical forests are cleared, there is a rapid switch in the dominant herbivore from wild sloths (suborder Folivora) to domestic cows *Bos taurus*. We quantified carbon dynamics for these mammals and the ecosystems they inhabit. Because of their low metabolic rates and photosynthetically-active algae, sloths emit trivial amounts of carbon (12 g C/sloth*day) compared to cows (2.3 kg C/cow*day). In parallel, forests are carbon sinks (-242 g C/m^2*year) and pastures sources (261 g C/m^2*year); cows contribute >50% of the net emissions from pastures. For a small farm in Costa Rica, this turnover in herbivores translates into ~166 metric tonnes of additional C emitted annually.

INTRODUCTION

Understanding the factors controlling carbon budgets has become globally, economically, and politically relevant. Carbon cycling has been viewed as an ecosystem-level function and, consequently, the role of individual species was largely ignored. It is increasingly recognised, however, that community composition and species interactions can have important ecosystem- to global-level effects on carbon dynamics (Schmitz et al. 2014). For example, grazing by ungulates shifting ecosystems from carbon sources to sinks (Holdo et al. 2009), forest die-offs from beetle eruptions releasing large quantities of CO_2 (Kurz et al. 2008), and trophic cascades induced by apex predators increasing autotrophic carbon sequestration (Strickland et al. 2013). While we have begun to account for the constituent effect of animals in carbon budgets (Schmitz et al. 2014), how land-use change interacts with the composition of hetero-trophs to alter ecosystem carbon emissions remains uncertain.

In many tropical forests of Central America, tree sloths (suborder Folivora) are the dominant mammalian herbivores (Eisenberg & Thorington 1973). As part of their arboreal lifestyle, sloths possess a suite of unique speciali-sations that allow them to overcome nutritional and energetic constraints associated with a diet composed almost solely of leaves (Pauli et al. 2014). For example, they have evolved ruminant-like organs to digest structurally complex and chemically protected leaves (Foley et al. 1995). Because of their nutritionally poor diet, sloths have an extraordi-narily slow rate of digestion (Foley et al. 1995), and to account for low energy accrual, sloths possess exceedingly low metabolic rates and the lowest daily energy expenditure recorded for any mammal (Pauli et al. 2016). Finally, as a consequence of their lifestyle strategy, sloths harbour a phoretic community of microbiota in their fur, including *Trichophilus* spp., a green alga found to grow only on sloths (Pauli et al. 2014).

When Neotropical forests are cleared, they are most frequently converted to pastures for livestock (Wassenaar et al. 2007). Accompanying this land-cover change is a pulsed release of carbon and, simultaneously, a rapid change in the vertebrate community, featuring the replacement of arboreal specialists with exotic species and terrestrial

generalists (Daily et al. 2003, Harris et al. 2012). Notably, there is a switch in the dominant mammalian herbivore from tree sloths in forest canopies to domestic cows *Bos taurus* stocked to pasturelands. Land conversion also features an important change in carbon cycling, as pastures are a sustained source of atmospheric carbon (Wolf et al. 2011). While the biotic and biogeochemical changes from tropical forest loss have been independently well-documented, how changes in species composition from forest conversion interact with carbon cycling and what that means for long-term ecosystem exchange of carbon remains virtually unexplored.

Given the suite of adaptations tree sloths have evolved to persist in an arboreal environment – in particular, a remarkably low respiration rate coupled with carbon uptake by phoretic algae – we predicted that the carbon footprint of a sloth would be negligible, especially in comparison to that of a cow. To test this prediction, we quantified all major carbon flux pathways for this dominant herbivore of many Neotropical forests, and then compared the resulting carbon budget to the carbon budget for the dominant herbivore of converted landscapes in Central America, the domestic cow. To explore the role of these species in carbon cycling, we then estimated net carbon exchange for the habitats in which they occur – tropical forest, shade-grown cacao, and cattle pastures. Finally, to assess the role of each species in carbon exchange at a practical scale, we estimated the role of cows and sloths in carbon emissions for a working farm in the Neotropics.

METHODS

To determine the carbon budget for three-toed sloths *Bradypus variegatus*, we identified the major pathways for carbon fluxes and converted these rates into standardised units (g C/individual*day). We estimated carbon fluxes from previous work conducted by our group and others (see Appendix S1), except for the net photosynthetic rate of the *Trichophilus* algae that sloths harbour. To estimate net carbon exchange of algae, we collected hair from sloths in March 2014 at our long-term field site in northeastern Costa Rica (10.32°N, −83.59°W). Animals were captured following previously-described procedures (Pauli et al. 2014), and 2–3 dorsal guard hairs were plucked from each animal and individually embedded into sterile agar slants in centrifuge tubes using sterilised tweezers. Fieldwork was authorised by Institutional Animal Care and Use Committee protocol A01424 through the University of Wisconsin-Madison. Access was granted by the landowner, our project was approved by the Ministerio de Ambiente, Energia y Telecomunicaciones, Sistema Nacional de Áreas de Conservación, Costa Rica, and samples were transported with the approval of the Convention on International Trade in Endangered Species of Wild Fauna

and Flora and the U.S. Fish and Wildlife Service. Multiple replicates of cultured algae in the centrifuge tubes were grown under the environmental conditions (light intensity, temperature, humidity; Appendix S1) experienced by sloths moving through the canopy at our study site for several months prior to estimating their carbon uptake by measuring oxygen concentrations in the centrifuge tubes every 5 min for a minimum of 36 h. We combined these estimates to determine the net carbon budget for an individual sloth, and then compared it to estimates that had been determined for the other dominant herbivore, the domestic cow (Appendix S1).

We estimated the density of three-toed sloths in each discrete habitat type that sloths utilise in our study site of intact tropical rainforest (26 ha), shade-grown cacao (130 ha), and cattle pastures (103 ha). Our study site is surrounded by monocultures (banana and pineapple), but given that neither cows nor sloths inhabit these land-use types, they were not included in subsequent analyses. Because juveniles make up a small component of the total sloth population and carbon emissions, we restricted our analyses to adults and subadults. We assumed that our long-term sloth capture efforts (initiated in 2010) achieved a complete population census within the delimited boundaries of our study site by 2013, and used the total number of marked subadult and adult sloths detected in each habitat in that year. Point estimates of density were calculated by dividing the number of marked sloths by the area of each of the three habitats. Beef cows were only kept in pastures at our site and we obtained a census estimate for cows from the landowner.

Using our estimates of animal density, average body mass, and carbon emissions, we calculated the contributions of sloths and cows to carbon pools (g C/m^2) and fluxes (g C/m^2*year) within intact tropical rainforests, shade-grown cacao, and cattle pastures. To quantify the magnitude of these two mammals in ecosystem-level carbon cycling, we obtained estimates of pools (g C/m^2) and fluxes (gross primary productivity, total ecosystem respiration and net ecosystem exchange; g C/m^2*year) from the literature for those same habitats (Appendix S1). To capture the range of values in carbon dynamics for Neotropical forests, we also estimated pools and fluxes for regenerating forests, even though they are not present on our study site but constitute an important land cover type regionally. Finally, we scaled our species-specific estimates of carbon emissions to a working farm in Costa Rica (Appendix S1).

RESULTS

We calculated that an individual sloth emits 12 g (2.9 g C/kg sloth*day) of carbon to the atmosphere in a day
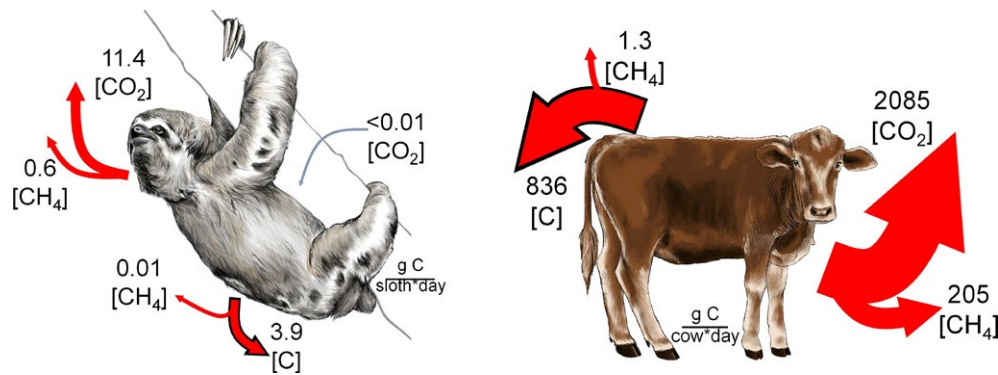
Fig. 1. Carbon budgets of sloths (left) and cows (right), dominant herbivores of Neotropical agro-ecosystems. Shown are carbon emitted, non-atmospheric contributions from excreta, and carbon sequestered by sloth algae. Units are g C/animal*day, and the form (CO_2, CH_4, or organic C) of each flux is shown in brackets. [Colour figure can be viewed at wileyonlinelibrary.com]

(Fig. 1a). In contrast, a cow emits 2.3 kg (4.2 g C/kg cow*day) of carbon per day – or >175 times more carbon than a sloth – principally from respiration and fermentation (Fig. 1b). The primary emission of carbon from sloths was via respiration, calculated to be 11.4 g C/sloth*day (2.8 g C/kg sloth*day), followed by methane released from foregut fermentation (0.6 g C/sloth*day [0.1 g C/kg sloth*day], Fig. 1a). An individual sloth also defaecates 3.9 g C/day, although this contributes a negligible amount of carbon in the form of methane (Fig. 1a). The carbon sequestered by algae in sloth fur constituted a minor component of the carbon budget. We are confident that our measurements of photosynthesis are realistic, albeit potentially conservative, because algae were cultivated with detailed local environmental conditions after months of acclimation and our estimates were similar to those obtained for other terrestrial algae (Ong et al. 1992).

In our study site, we identified 59 individual adult and subadult three-toed sloths, which translated to densities of 1.2 sloth/ha, 0.12 sloth/ha, and 0.07 sloth/ha in intact tropical rainforest, shade-grown cacao, and cattle pasture, respectively; 200 cattle were kept on the pasture (1.9 cows/ha). Both species constituted trivial pools of carbon in the ecosystem (i.e., <0.2%) after accounting for carbon held in plants and soils (Fig. 2). In terms of fluxes, rainforests were large sinks for carbon (with regenerating forests sequestering the most carbon), while shade-grown cacao and especially pastures were sources of atmospheric carbon. For all habitats, the carbon emission of sloths was trivial in ecosystem exchange of carbon. Cows, on the other hand, were significant sources of atmospheric carbon, contributing over half of the net ecosystem carbon in pastures (Fig. 2).

When scaled to the area of the working farm, the total sloth population emitted approximately 0.7 kg C/day, compared to cows, which emitted 460 kg C/day on the farm, a four orders of magnitude difference in total C

emissions. Altogether, then, the switch in the dominant herbivore – from sloths to cows – increased overall carbon emissions by 166 metric tonnes C/year for the farm.

DISCUSSION

The conversion of tropical forest to pasture results in an important switch in mammalian herbivores, which significantly contributes to net carbon exchange. We found that sloths were effectively carbon neutral, and that the transition from sloths to cows, which is occurring throughout Central America alongside land conversion (Wassenaar et al. 2007), led to notable increases in carbon emissions at the scale of a multi-use farm in Costa Rica. Recent models have begun to account for global cattle methane emissions (e.g., Tian et al. 2016), but there have been few downscaled estimates for total carbon emissions resulting from livestock production, especially compared to the carbon emissions of the native herbivores that originally inhabited these sites.

Our findings highlight the importance of the often-overlooked role of individual species – especially certain vertebrate heterotrophs – in contributing to the net ecosystem exchange of carbon. Indeed, we estimated that cows alone contribute over half of the net carbon exchange for pastures in Central America, and that the 200 cows raised within a single farm at our study site can contribute a significant amount of carbon annually (166 metric tonnes C/year). Our findings also reveal that land use conversion in Neotropical forests, in addition to releasing large quantities of previously sequestered carbon in biomass and soils, can indirectly provide a sustained source of carbon by altering community composition in vertebrate herbivores.

Latin America has one of the highest deforestation rates in the tropics, and deforested land is predominantly converted to pastures for grazing (Wassenaar et al. 2007). While
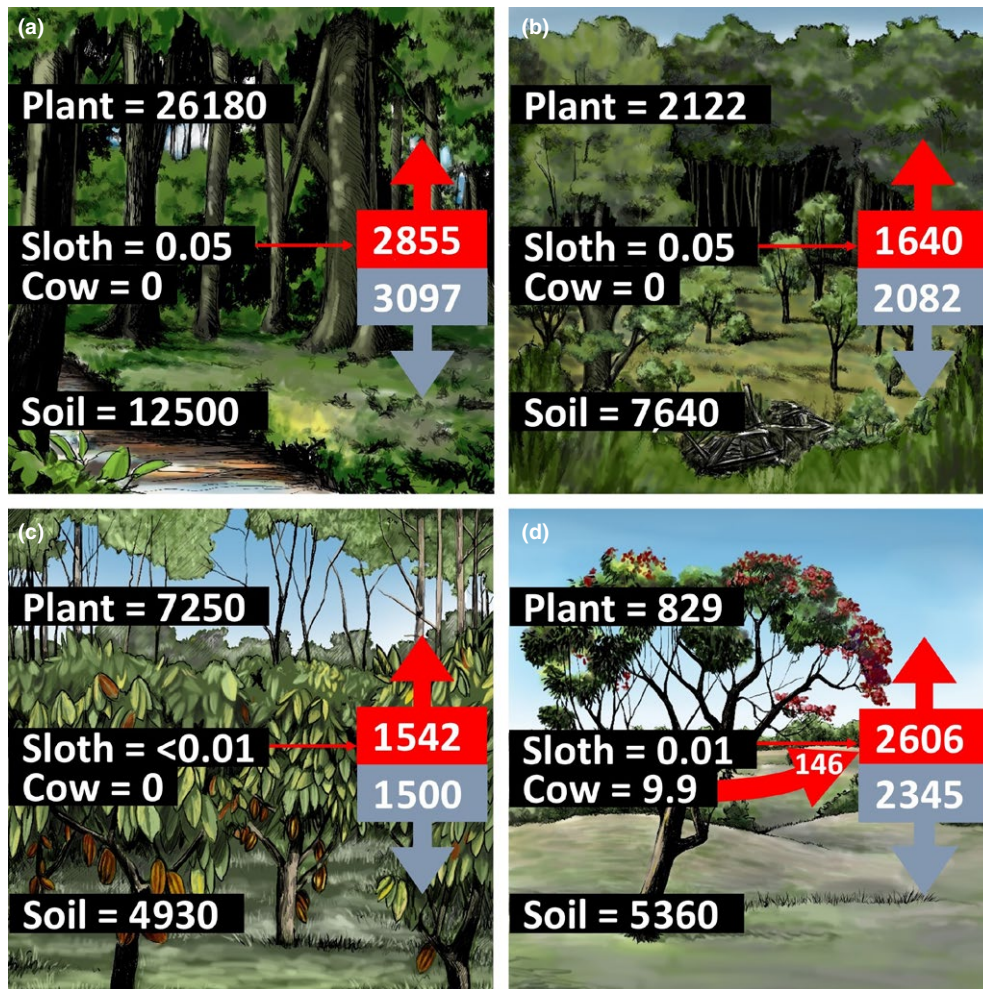
Fig. 2. Carbon pools (boxes; g C/m^2) of plants, soils, cows and sloths in four major habitat types in the Neotropics: (a) intact tropical rainforest, (b) regenerating forest, (c) shade-grown cacao and (d) cattle pasture. Also shown are carbon fluxes (g C/m^2*year): gross primary productivity (downward arrows) total ecosystem respiration (upward arrows), and the amount of carbon emitted from cows and sloths (g C/m^2*year). Sloths contribute trivial amounts of net ecosystem carbon (<0.3%), while cows emit 146 g C/m^2*year, or 56% of net carbon emission in pastures. [Colour figure can be viewed at wileyonlinelibrary.com]

conservation biologists have independently accounted for the immediate impact of habitat degradation on biodiversity (Gibson et al. 2011) and carbon exchange (Harris et al. 2012), the implicit links between the two, and the role of mammals in carbon cycling, has been mostly ignored. Nearly every country is now required to assemble detailed inventories of carbon emissions and plans to minimise them. Our work highlights the unique role that organisms have on carbon budgets and how the effects of land-use change on species assemblages can further intensify and provide sustained carbon emissions from deforestation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Supplementary methods and results.