Analysis

Carbon Costs and Bushmeat Benefits of Hunting in Tropical Forests

Jedediah F. Brodie

Division of Biological Sciences & Wildlife Biology Program, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA

A B S T R A C T

Unsustainable hunting is widespread globally, generating one of the primary threats to tropical vertebrates but providing important revenue for many people. Recent evidence suggests that by removing seed dispersing vertebrates, overhunting can induce shifts in tree species composition that reduce the amount of carbon stored in the forest. I developed a bioeconomic model to assess the conditions under which hunting might lead to the loss of forest carbon, and to compare the revenue lost via carbon erosion to that gained from bushmeat procurement. The potential long-term decline in forest biomass and the uncertain degree of ecological complementarity among frugivore species had the strongest influence on the amount of carbon lost via overhunting. Parameters related to frugivore population dynamics and the economics of the hunting system had relatively little influence. Total revenue in the system was maximized when hunter effort and the opportunity costs of hunting were low, suggesting that limiting hunting effort could maximize income for hunters by avoiding the depletion of both game species and potentially saleable carbon credits. These results highlight that enhanced understanding of long-term carbon responses to hunting in different tropical forests could help increase revenue for forest-dwelling people and contribute to global climate change mitigation efforts.

1. Introduction

Overhunting is nearly ubiquitous in tropical forests. Because many of the hunted animals are important dispersers of plant seeds (Redford, 1992), hunting-induced declines and outright extirpations of frugivores can have cascading impacts on plant recruitment (Brodie et al., 2009a). But while some plants might be negatively affected by loss of their seed dispersers, others (for example those with abiotic seed dispersal) may be unaffected by hunting, or even benefit via reduced competition with biotically dispersed species (Terborgh et al., 2008; Harrison et al., 2013). Hunting can therefore lead to shifts in the species composition of tropical tree assemblages (Terborgh et al., 2008; Harrison et al., 2013).

Recently it has emerged that the impacts of hunting could cascade ever farther -affecting not just tree populations and communities, but the forest ecosystem. In particular, because tropical tree species vary greatly in their size (Osuri et al., 2016) and the density of their wood (Chave et al., 2009), shifts in tree species composition in overhunted areas could alter the total biomass of the forest and therefore the amount of carbon that it stores. Simulations using demographic data from tree plots suggest that hunting could reduce forest carbon storage by 2–12% in Latin America and Africa (Osuri et al., 2016), potentially as high as 38% in portions of the Amazon Basin (Peres et al., 2016). Measurements of size and wood density in different tree age classes in Gabon indicated 15% declines in aboveground forest carbon in unsustainably hunted areas (Poulsen et al., 2013). Tropical forests store huge amounts of carbon, so if these cascading impacts are representative of general patterns, the hunting of vertebrates in tropical rainforests could affect the global carbon cycle and hamper efforts to mitigate climate change (Brodie and Gibbs, 2009; Brodie, 2016).

However, our understanding of this potentially crucial issue is still very limited. Our knowledge about the ecological relationships between frugivorous vertebrates and tree community traits is in its infancy, limiting our ability to predict how much carbon might be lost from overhunting in different areas (Brodie, 2016). Moreover, the issue has never been placed in a bioeconomic context. A primary strategy by which the hunting-induced loss of forest carbon could be reduced would be for international programs such as REDD+ (Reduced Emissions from Deforestation and forest Degradation) to limit hunting (Brodie, 2016). But hunting provides important revenue to local people, either by providing products for sale in markets or by providing subsistence food that reduces the need to purchase or utilize other foods (Milner-Gulland and Bennett, 2003; Corlett, 2007; Harrison et al., 2016). So revenue that is potentially lost by hunting-induced erosion of forest carbon must be compared to the revenue gained by the hunting itself. But to date no studies have attempted to do this.

While it could be argued that sustainable hunting may be necessary for both forest carbon storage and long-term hunting yields, there are two important complications. First, because we know so little about how frugivore density affects tree community traits such as mean size or wood density (Brodie, 2016), we do not know whether hunting levels

that were sustainable in terms of not driving the frugivores extinct were also able to maintain animal densities at levels sufficiently high enough to avoid significant erosion of forest carbon. Second, maintaining long-term hunting yields may or may not actually be in the economic best interests of the hunters. When the economic discount rate is relatively high, for example, the rational decision for hunters would be to harvest the animals to extinction quickly and invest the funds at a high rate of return (Clark, 1990; Ludwig, 2001).

Here I develop a bioeconomic model to compare the economic costs (via lost carbon) and benefits (via meat procurement) of hunting frugivores in tropical forests. I searched the published literature to find value ranges to parameterize the model. As discussed above, our understanding of much of the ecology and economics of the system is very poor. Therefore, rather than trying to generate exact predictions of costs and benefits, I assess the conditions under which revenue from carbon and hunting might outweigh each other, and ask where our (substantial) uncertainty in the various parameters most limits our predictive ability. In particular, I address the following objectives:

1) Determine the factors that influence how much carbon might be lost via overhunting.

2) Assess how we can maximize total revenue (from hunting plus forest carbon storage).

2. Methods

Most hunting in tropical forests is unsustainable, leading to depletion or extirpation of medium- and large-bodied animals (Milner-Gulland and Bennett, 2003; Harrison et al., 2016). When logging or road construction provide new access to previously remote areas, hunting can rapidly deplete vertebrate biomass (Robinson et al., 1999; Robinson and Bennett, 2000). I modeled the annual decline in the density (biomass) of large vertebrates ($\frac{dD}{dt}$, in kg y^{-1}) exposed to over-exploitation with a modified Gordon-Schaeffer function (modified by the inclusion of a θ shape parameter, as discussed below):

$$\frac{dD}{dt} = R_{frug} D_t \left(1 - \left[\frac{D_t}{D_0}\right]^\theta\right) - qED_t \tag{1}$$

where R_{frug} is the intrinsic rate of change in frugivore density in the absence of hunting or competition, D_t is frugivore density in year t (ranging from D_0, the original biomass of medium- to large-sized frugivores in a given tropical forest ecosystem, to D_T, the final biomass after exploitation over a given time period T), q is the catchability coefficient of the frugivores, E is hunter effort, and θ is a shape parameter controlling the expression of density dependence in the frugivores (Sibly et al., 2005). See Table 1 for ranges of these (and other) parameter values. The product qE is the proportional exploitation rate of frugivores, making this model equivalent to the theta-logistic proportional harvest model (Ludwig, 2001).

I estimated the total income generated from hunting (in 2015 USD km^{-2}) over time period T as:

$$Income_{hunting} = \sum_{t=1}^{T} (qED_t)(\delta^{T-t})(P_{bushmeat}) \tag{2}$$

where $P_{bushmeat}$ is in 2015 USD per kilogram and δ is the economic discount rate (Table 1). The costs of hunting were measured, following the Gordon-Schaeffer model, as the product of annual hunter effort (E) and per-unit-effort cost (a), discounted over time based on δ. Per-unit-effort costs were the opportunity costs of not engaging in paid employment (Table 1), standardized to a per-area unit (km^{-2}) based on human population densities in hunted tropical forests (Bennett and Robinson, 2000; Hill and Padwe, 2000; Robinson and Bennett, 2000). Hunting revenue ($Revenue_{hunting}$) was then $Income_{hunting}$ minus total costs.

The forest carbon remaining at time T (C_T; t km^{-2}), as a function of declines in frugivore density, was estimated with a power function:

$$C_T = B_{Forest} - (B_{Forest} L_{max})(1 - F_T{}^z) \tag{3}$$

where B_{Forest} is the aboveground biomass of carbon in the forest in t km^{-2}, L_{max} is the maximum proportional loss (if any) of forest carbon if frugivores are completely removed from the system, F_T is the proportion of the original frugivore density still remaining at time T, and z is a shape parameter modeling frugivore complementarity. Declines in frugivore density could reduce forest carbon linearly ($z = 1$) if zoochorous tree regeneration depends strictly on the quantity of seeds dispersed and all frugivore species are equivalent in their dispersal services. At $0 < z < 1$, initial declines in frugivore density (i.e. when animals are still close to carrying capacity) would have less influence on forest carbon storage than do declines when frugivore density is already low because, for example, functional redundancy among species (Brodie et al., 2009b) is still present at high densities. Alternatively still, frugivore declines could have strong effects on carbon initially ($z > 1$) if the species that provide the most or the highest quality seed dispersal (e.g. the largest mammals) are driven extinct first, as is often the case in overhunted tropical forests (Brodie et al., 2009b; Peres et al., 2016).

The proportional change (if any; ΔC) of carbon from the forest due to hunting was then calculated by:

$$\Delta C = \frac{C_T - B_{Forest}}{B_{Forest}} \tag{4}$$

and the revenue loss, in 2015 USD km^{-2}, from any hunting-induced erosions of forest carbon storage was estimated as:

$$Revenue_{carbon} = [B_{Forest} - (B_{Forest} \times \Delta C)](P_{carbon}) \tag{5}$$

where P_{carbon} is in 2015 USD t^{-1}. I performed literature searches to assess the potential values for the parameters in the model (Table 1). Then, for each of 1 million model runs, I randomly drew parameter values from uniform distributions bounded by the extreme values (see Table 1).

To address the study objectives, I used multiple regressions to compare the relative influence of each of the parameters in Table 1 (independent variables) on two dependent variables: (1) the carbon lost from the system (ΔC; Objective 1), and (2) the total revenue obtained from the system, or $Revenue_{hunting} + Revenue_{carbon}$ ($Revenue_{total}$; Objective 2). The randomly generated parameter values from the model runs were standardized to have means of 0 and variances of 1 so that their model coefficients could be directly compared. I also report the strength of the relationships (measured as R^2 values from univariate regressions) between each parameter and the two dependent variables (cf. Mills et al., 1999; Wisdom et al., 2000).

3. Results

For Objective 1, the carbon lost (if any) from the system via overhunting-induced shifts in tree species composition was most strongly related the maximum potential biomass change following complete extirpation of frugivores (L_{max}; $\beta = -0.77$; Table 2). Functional compensation among frugivores (z) was also related, though less strongly ($\beta = -0.29$), to the amount of lost forest carbon. Parameters related to the population dynamics of frugivores in the face of hunting, including the intrinsic rate of increase (R_{frug}; $\beta = -0.03$) and the unhunted density of frugivores (D_0; $\beta = -0.001$) had little or negligible relationship with forest carbon change. Likewise, parameters associated with the hunting system, including frugivore catchability (q; $\beta = -0.06$), hunter effort (E; $\beta = -0.11$), and the opportunity cost of hunting (a; $\beta = 0.001$) had relatively weak influence on forest carbon change.

For Objective 2, hunter effort (E; $\beta = -0.20$), the opportunity cost of hunting (a; $\beta = -0.13$), and the price of bushmeat ($P_{Bushmeat}$; $\beta = 0.11$) had the strongest influence on the total revenue ($Revenue_{Hunting} + Revenue_{Carbon}$) generated by the system (Table 2); revenue increased when hunter effort was low. Parameters that were