

from Brahman (*Bos indicus***) breeding herd systems based on long-term research on**

24 to raise and breed tropical beef heifers and cows, and their impacts on methane $(CH₄)$ emissions and overall carbon (C) footprint are still unknown. This study aimed to predict CH⁴ emissions, animal-environmental metrics and overall C footprint across heifers' growth, cow-calf-bull and cull cows' fattening productive stages of Brahman (*Bos indicus*) breeding herds, lifetime-grazing on *B. decumbens* pastures or a sequence of native savanna and *B. decumbens* pastures. A dynamic model-method was used with detailed liveweight (LW) and productive lifetime-cows' data together with estimated values of above- and belowground pasture biomass and soil C stocks. This framework recognized commercial farming practices such as growing and mating female herds on Bd (Bd scenario) or rising them on savanna and grazing Bd pastures (SaBd scenario) during the herd's breeding life. The study complemented this socio-economic, cultural and productive tradition by fattening cull cows using the improved Bd pasture and illustrated the cointegrating relationship with structural-flows of LW-derived CH⁴ emissions. As heifers aged, accumulated CH⁴ emission efficiencies [t carbon dioxide (CO_2) equivalent $(CO_2$ -eq) head ⁻¹] were lower in the Bd scenario than in the SaBd 39 scenario from birth to conception $(2.67 \pm 0.087 \text{ vs } 3.49 \pm 0.087; P < 0.0001)$, while following the same trend, emissions from the first to the fourth lactation were in the range of 0.821-0.865 (*P* < 0.05) between scenarios, but similar in the two other lactations. 42 Methane efficiency estimates from cow-calf pairs (t CO_2 -eq kg⁻¹ calf born) tended to be lower in the Bd scenario than in the SaBd scenario up to the fourth lactation. In the 44 extreme, calculated values during the fattening phase were 0.935 t CO₂-eq head $^{-1}$. In this context, the estimated animal greenhouse gas emissions and annual soil C accumulation values revealed not only a differentiation of the estimated C footprint at system level 47 between animal productive stages, but also more likely natural $CO₂$ removal from the atmosphere with all three animal phases of Bd scenarios. Hence, this study provides evidence for the experimental hypothesis that dynamic modelling based on long-term research results on improved Bd pastures would allow the estimation of the overall C footprint of Brahman breeding herds and their sustainable performance in the Colombian neotropical savanna environment.

Keywords

liveweight, Orinoco basin, reproductive performance, soil emissions, tropical grass

1. Introduction

 Livestock production as a contributing factor of global warming has become a critical component of judgment and policy development amongst scientists, institutions, governments and societies [Food and Agriculture Organization of the United Nations (FAO), 2006, 2015; Intergovernmental Panel on Climate Change (IPCC), 2019; Fletcher and Schaefer, 2019].

 Nevertheless, generalizations in this regard are fraught with difficulties regarding the effects of pasture management (Dini et al., 2017; Chirinda et al, 2019), and animal genetics and management (O'Neill et al., 2013, 2016; Florindo et al., 2017; Oliveira et al., 2018) among others. Also, there is wide recognition of the need to intensify land use and animal production (Cardoso et al., 2016). This is to satisfy an increased demand for animal products in developing countries with implications for not only ensuring food, nutrition and health security, but also protecting the environment as part of sustainable development goals [FAO, 2013; Lê Đình et al., 2015; Lê Đức et al., 2015; High Level Panel of Experts for Food Security and Nutrition (HLPE), 2016; Ramírez-Restrepo et al., 2017, 2019a].

 Improving animal performance in tropical countries is a key strategy to meet the demand for animal protein, while reducing greenhouse gas (GHG) emissions and improving resource use efficiency (Rao et al., 2015; Cardoso et al., 2016; HLPE, 2016). There are opportunities to improve and sustain animal performance through animal

 genetics, animal health, quantity and quality of feed and animal nutrition. Surprisingly, there are few studies on improved pastures that have conceptualized and integrated complementary grassland resources for sustainable ruminant production with reduced carbon (C) footprint, particularly under year-round grazing conditions (Ramírez-Restrepo and Barry, 2005). Interestingly, some of these studies are based on IPCC Tier II algorithms (Cardoso et al., 2016; Florindo et al., 2017) with its attending uncertainties (Goopy et al., 2018).

 Under such conditions, the challenge for researchers is to articulate how sustainable grassland management practices could deliver a number of ecosystem services. These include: (i) cultural dimensions of livestock; (ii) water (quality, quantity and flow); (iii) 85 provisioning (animal products); (iv) supporting [forage production, nitrogen (N_2) fixation, nutrient cycling through plants and animal excreta]; and (v) climate regulating [soil organic C (SOC) accumulation, GHG emissions from soil and ruminants] services to benefit resource-protection, biodiversity and sustainable intensification of agriculture (Rao et al., 2015; Bengtsson et al., 2019; Sollenberger et al., 2019). Therefore, the potential of grasslands to contribute to multifunctional landscapes and to food security and sustainable livelihoods can be greatly enhanced by integrating grasslands into agricultural production systems and by making land-use decisions at the local and regional level (Bengtsson et al., 2019).

 This is especially relevant to the extensive grazing systems in the eastern plains of 95 Colombia (i.e. Llanos; ~17 million ha), a landscape inhabited by ~ 1.7 million of native (i.e. *llaneros*), colonial and indigenous socio-cultural diverse people [Navas-Rios, 1999; Tapasco et al., 2015, Departamento Nacional de Estadística (DANE), 2019]. The 98 livelihoods of these persons are linked to \sim 5.1 million heads of beef breeding cattle grazing on ~ 9.4 million ha of neotropical savannas in which sown *Brachiaria* grass

 pastures have been introduced [Tapasco et al., 2015; Federación Colombiana de Ganaderos (FEDEGAN), 2019]. Knowledge on the biology, agronomy, and improvement of *Brachiaria* species and cultivars and the advantages and disadvantages of the use of these grasses in the Llanos and other tropical regions is compiled in detail by the International Center for Tropical Agriculture - Empresa Brasileira de Pesquisa Agropecuária [(CIAT-EMBRAPA), 1996] and Miles et al. (2004). In this context, proper implementation of grasslands' technology adaptation and transfer should not only improve year-round cattle production, agro-industrial supply chains and socio-economic drivers (Velasquez, 1938; CIAT, 1982, CIAT-EMBRAPA, 1996), but can also lead to a more sustainable farming future (CIAT, 2014).

 The traditional, but evolving use of the Colombian neotropical savannas in the Orinoco basin revolves around cattle breeding systems that rely on the native grasslands with occasional use of sown grass pastures [Corporación Colombiana de Investigación Agropeacuaria (AGROSAVIA), 2019]. Indeed, the tradeoffs between the reproductive performance of Brahman (*Bos indicus*) and crossbred Brahman herds grazed on savanna plus sown (improved) pastures (Vera and Ramírez-Restrepo, 2017) of *B. humidicola* (Rendle) Schweick (syn. *Urochloa humidicola* ; Vera et al., 1993) and *B. decumbens* Stapf (syn. *U. decumbens*; Vera et al., 2002) have become increasingly important (Vera and Hoyos, 2019; Vera-Infanzón and Ramírez-Restrepo, 2020) in comparison with savanna-based breeding herds (Rivera, 1998). Ramírez-Restrepo et al. (2019a) used 4-5 years of field data to estimate C balance based on C emissions from GHGs and C accumulation in soil (i.e. C footprint) of conventional weaning herd systems in savanna, and found that the use of savanna combined with strategic use of improved pastures for early weaning herd systems led to improved balances. Furthermore, Vera and Ramirez-Restrepo (2017) reported that the strategic grazing of improved pastures by early weaned calves reduced the subsequent inter-calving period of their Brahman and crossbred Brahman cows grazing on savanna leading to improve production efficiency.

 Nevertheless, there is no knowledge of the effects of alternative combinations of native savanna and improved pastures to raise and breed tropical beef heifers and cows, and the corresponding effects on methane (CH4) emissions and C footprint. This includes the assessment of breeding herd dynamics using pure stands of *B. decumbens* and *B. humidicola*. The pure stands of these improved pastures with proper grazing management are known to contribute to increased animal production (Lascano, 1991) and soil C accumulation (Fisher et al., 1994; Rondón et al., 2006). In particular, the use of C isotope ratios allowed to demonstrate that soil C accumulated under the improved pastures replaces some of the soil C from native savanna pastures (Rao et al., 1994). Improving animal production efficiency with the strategic use of introduced pastures in extensive beef production systems of tropical savannas has significant agricultural and environmental implications. This means not only improving animal productivity, but also reducing C footprint through mitigation of enteric CH⁴ emissions from animals and 140 nitrous oxide (N_2O) emissions from animal discharges (urine and feces) and soil; and increasing soil C accumulation at system level (Castaldi et al., 2006; Rondón et al., 2006; Rao et al., 2015; Cerri et al., 2016; Ramírez-Restrepo et al., 2019a).

143 The objective of this study was to estimate the lifetime CH₄ emissions, animal- environmental metrics and overall C footprint across heifers' growth, cow-calf-bull and cull cows' fattening productive stages of Brahman (*Bos indicus*) breeding herds, based on long-term research on grazing of *B. decumbens* pastures or a sequence of native savanna and *B. decumbens* pastures. To achieve this objective, the study compared the common productive strategy of raising replacement heifers on native savanna up until reaching mating liveweight (LW) followed by breeding on improved *B. decumbens*

 pasture, with a more intensive system relying exclusively on this sown grass. At the end of their reproductive life, cows were fattened and culled after grazing on *B. decumbens* pastures to assess their contribution to CH⁴ emissions and complete the birth to exit cycle from the production systems.

 The hypothesis tested was that the retrospective use of time-dependent change data from field experiments to perform dynamic modelling should further increase information about CH⁴ emissions, animal-environmental metrics and the estimated C footprint of breeding herds grazing on neotropical savannas complimented with improved pastures. This hypothesis was tested to address the common prejudice that questions the environmental limitations and sustainable future of the savanna beef industry in Colombia and elsewhere.

2. Materials and methods

2.1. Description of data used for modelling

 The study used a commercial Brahman herd dataset for 1979-1988 involving 164 individual lifetime records of 30 heifers born and raised up (272.6 \pm 2.94 kg vs 25.87 \pm 0.635 months) on neotropical savanna and seasonally bred on *B. decumbens* covering a period of 12 years. These data were sourced at Carimagua Research Centre (CRC: 167 4°36'44.6" N latitude, 74°08'42.2" West longitude) in the Meta Department of Colombia (Vera et al., 2002). Readers are referred to Vera and Ramírez-Restrepo (2017) for detailed climatic information at CRC from 1979 to 1991.

2.2. Pastures

 Weaned female calves, later heifers, were raised on native savanna paddocks stocked 172 at 0.2 AU ha⁻¹, subjected to continuous grazing and supplemented with a complete mineral lick as described by Ramírez-Restrepo et al. (2019a). In contemporaneous studies 174 and at the same location, Rao et al. $(2001a)$ also quantified average aboveground yield of forage biomass available on offer, and the belowground root biomass accumulation on these savannas.

 The *B. decumbens* pasture was established two years prior to the start of the 178 experiment, using the recommended fertilizer application (kg ha $^{-1}$) consisting of 20 P 179 (applied as P₂O₅), 20 K (applied as K₂O), 48 Ca, 14 Mg and 10 S. During the fourth year of the experiment, the pasture was renovated with a superficial disking and received the recommended maintenance fertilizer application consisting of one third of the rate used at the time of pasture establishment followed by a six weeks of rest period. Nevertheless, and for the purpose of the present analyses, a more conservative approach was followed with the assumption that the pasture maintenance operations of disking and fertilization were carried out every three years. This was the observed median frequency recorded in a farm survey (Vera et al., 1998).

 Grazing was continuous and the average stocking rate (SR) consisting of cows and 188 their suckling calves (9 months year $^{-1}$), and 2 bulls (6 months year $^{-1}$) amounted to 1.5 189 animal units (AU; kg) ha⁻¹. This allowed the pasture to maintain a height of 15-25 cm that falls within the generally recommended condition for sustained animal production in tropical grasses with decumbent growth habit (Gomes et al., 2018).

2.3. Database

 The gathered dataset file has never been used to assess CH⁴ emissions and for the purpose of this study, we extended it by adding two-years of CRC relevant unpublished 195 animal records from the same animals. The data included birth dates, mortalities, branding numbers and LWs at birth, mating, conception, gestation, calving and weaning across six continuous RCs (conception to weaning unless otherwise noted). Insufficient numbers 198 precluded the use of the seventh RC. Calves were weaned at 8.89 ± 0.144 months of age. No voluntary cow culling was practiced; the trade-offs of following this practice were discussed by Roberts et al. (2015) and will be addressed in the near future. Cattle had always free access to fresh water and to a commercial mineral supplement containing as-202 fed (g kg⁻¹) 137 Ca, 269 Cl, 0.01 Co, 1.038 Cu, 0.076 I, 175 Na, 80 P, 20 S and 3.5 Zn. The longitudinal study was conducted in accordance with the Colombian animal husbandry and animal welfare regulations and it was permanently monitored by on-CRC national registered Doctors of Veterinary Medicine.

2.4. Model and estimation equations

207 The structural-flow of LW-derived CH₄ emissions was calculated using an Excel® spreadsheet dynamic model which combines the mechanistic modeling. This was conceptualized and developed by Ramírez-Restrepo and Vera (2019), Ramírez-Restrepo and Vera-Infanzón (2019), and Ramírez-Restrepo et al. (2019a, 2019b) based on linear regressions between LW and dry matter intake (DMI; Eq. 1) and between LW and CH⁴ 212 emissions (g day $^{-1}$; Eq. 2). Equations derived from pooled data from Brahman and Belmont Red Composite [Africander (African Sanga) x Brahman x Hereford-Shorthorn (3/4 *B. taurus*)] steers (*n* = 18) fed *ad libitum* [2.1% of total LW (Fisher et al., 1987)] on a non-supplemented DM basis in open-circuit chambers (Ramírez-Restrepo et al., 2014, 2016a, b).

- Eq. 1.
- 218 DMI = 2.216 (\pm 1.315) + 0.014 (\pm 0.003) LW
- *r* 2 = 0.491, *P* < 0.01; CV = 18.94; r.s.d = 1.34; r = 0.701, *P* < 0.01
- Eq 2.
- 221 CH₄ (g day ⁻¹) = 16.176 (\pm 21.087) + 0.324 (\pm 0.057) LW
- 222 $r^2 = 0.663$, $P < 0.0001$; CV = 16.78; r.s.d = 30.82; r = 0.814, $P < 0.0001$;

2.5. Assumptions

 The study used Eq.1 for suckling calves after 56 days of age, while over the last 75 days of the standard gestation period (285 days), females were fed at 1.8% of total LW to reflect the variation of DMI during late gestation (Johnson et al., 2003). In parallel, Eq. 2 was used to estimate LW-derived CH4 emissions after 56 days of age (Rey et al., 2014; Huws et al., 2018), while pre-weaning gestation emission values with lactation emission values were overlapped on the same animal to avoid double counting.

230 Carbon dioxide (CO_2) equivalent $(CO_2$ -eq) indices were computed to provide constant emission values using the average value of 34 as the relative GHG global warming 232 potential (GWP) of CH_4 in the atmosphere as an established timescale function of 100 years. This parameterization effect includes climate C-feedbacks, which consider change in the magnitude of terrestrial and ocean C uptake in response to sustained or variable climate background (Myhre et al., 2013; Gasser et al., 2017; Mueller and Mueller, 2017).

 As Ramírez-Restrepo and Vera (2019), Ramírez-Restrepo and Vera-Infanzón (2019) and Ramírez-Restrepo et al. (2019a) pointed out, the results derived from the model can be scaled up to emissions per area, AUs, variable SRs, and CH⁴ energy (MJ) losses 239 (Ramírez-Restrepo et al., 2020). The latter by converting CH₄ emissions to energy mass 240 density (55.6 MJ kg $^{-1}$ CH₄; Bossel and Eliasson, 2002).

2.6. Scenario development

 Two production scenarios [i.e. savanna plus *B. decumbens* (SaBd) pasture and *B. decumbens* (Bd) alone pasture] were analysed that differ in the management of female weaners, later heifers, prior to the start of the breeding phase. The boundaries of the systems analysed are presented in Fig. 1.

 Fig. 1. Flow diagram of the boundaries of the systems with inputs on top, and outputs in the bottom for three different phases (i.e. growing heifers, breeding, and fattening of cull cows) of Brahman beef cattle herds. Growing heifers were grazed on either *Brachiaria decumbens* (Bd) pasture or native savanna until mating. Thereafter, all breeding cows and their calves, were grazed exclusively on *B. decumbens* pastures, and upon culling, cows were fattened on the same pasture. The blue diamond represents decision- making 253 regarding time of culling. Nitrous oxide (N_2O) and methane (CH_4) emissions, and the C 254 balance of each system were estimated, to derive an overall C footprint of both scenarios that are included in Table 5.

 The SaBd scenario assumes that as is most frequently the case, heifers are grazed on native savanna following weaning until they reach a target LW of 272 kg. The Bd scenario assumes that heifers are weaned and raised on *B. decumbens* pastures until reaching the same threshold LW, representing a more management intensive system. Thereafter, animals in both scenarios are maintained on *B. decumbens* pasture for the duration of the nine years of breeding phase.

262 The model did not address at this stage the impact of CH₄ emissions from replacement heifers born and raised after the second conception, to maintain the herd size after the second lactation, but based on present estimates, that more complex scenario could be simulated. Similarly, it was inferred that all calves are sold at weaning. However, CH⁴ emissions estimations from cull cows fattened on *Brachiaria* pastures were calculated (Ramírez-Restrepo and Vera, 2019) to complete the systems boundary (Fig. 1), and to estimate total life emissions and derived animal-environmental metrics at the farm gate.

 Daily CH4 emissions (i.e. 210.8 g) from Brahman bulls (Mean; 600 kg LW) mated at a male to female ratio of 2:30 in early (April-May, 45 days) and mid-late (August- October, 90 days with bulls' replacement on day 60) wet season in each year were 272 excluded from both herd emissions and shipped to the overall C footprint estimation since 273 they are comparatively small (Ramírez-Restrepo et al., 2019a). The $CO₂$ -eq costs associated with pasture establishment and renovation (i.e. use of machinery and 275 fertilizers) were included to estimate C footprint in $CO₂$ -eq in both scenarios. The Bd pastures are assumed to be productive well over 10 years with the above described management practices, as demonstrated by Lascano and Estrada (1989) among others.

2.7. Complementary equations and model implications

 The LW evolution of heifers from birth to weaning was calculated based on field data using random individual birth LWs and age (days) at weaning from heifers calved (28.6 281 \pm 0.53 kg) and weaned (237 \pm 4.40 days) by their corresponding experimental cows on

282 Bd. Next, Eq. 3 derived from *B. decumbens* pooled data (*n* = 413; Vera et al., 2002) was

283 used to compute retrospectively the weaning LW (164 ± 2.82 kg) of those cows.

284 Eq 3.

285 Weaning LW = 34.074 (\pm 1.497) + 0.532 (\pm 0.097) age (days)

286 $r^2 = 0.879$, $P < 0.0001$; CV = 19.58; r.s.d = 51.57; r = 0.937, $P < 0.0001$

 Individual heifers' body growth was subsequently modelled from weaning to the 288 beginning of the first breeding season (16.37 \pm 0.635 months) assuming a daily LW gain 289 (LWG) of 428 ± 9.76 g. This daily rate was based on LWGs reported from the use of same pasture on-farms (Vera and Hoyos, 2019) and the growth difference (16.9%) between heifers and yearlings grazing together and contemporaneously on *Andropogon gayanus*-based pastures at CRC (Ramírez-Restrepo and Vera, 2019); and these values were further supported by LWGs reported for young steers by Lascano and Estrada 294 (1989).

295 In parallel, females born $(26.0 \pm 0.53 \text{ kg})$ and lactation length $(271 \pm 4.40 \text{ days})$ of 296 their producing cows at weaning taken from savanna pooled data $(n = 19)$; Rivera 1988; 297 Vera and Ramírez-Restrepo, 2017; Ramírez-Restrepo et al., 2019a) were individually 298 apportioned to each heifer before mating on *B. decumbens* pasture. In this context, Eq. 4 299 which describes the relationship between weaning LW and lactation length that was 300 applied, whereas LW value of 241 ± 9.76 g day ⁻¹ (Vera and Hoyos, 2019) were used 301 from weaning (157 \pm 2.82 kg) to individually achieve the initial LW of the first breeding 302 season.

303 Eq 4.

304 Weaning LW = 24.944 (\pm 17.512) + 0.487 (\pm 0.095) lactation length (days)

305 $r^2 = 0.606$, $P < 0.0001$; CV = 24.21; r.s.d = 32.77; r = 0.778, $P < 0.0001$

2.8. Estimation of carbon stocks and carbon footprint in CO2-eq

307 The values used to estimate C stocks and C footprint in $CO₂$ -eq of the native savanna were adapted from Ramírez-Restrepo et al. (2019a) with slight modifications as follows. 309 Methane and N_2O emissions from feces and urine were calculated using locally derived 310 estimates (Byrnes et al., 2017) and checked against literature values values (Lopez- Hernandez and Hernandez-Valencia, 2008; Copeland et al., 2012; Waldrip et al., 2013; Lessa et al., 2014; López-Hernández et al., 2014; Mazzetto et al., 2014; Fischer et al., 313 2016; Valadares Filho et al., 2016). Methane emissions from feces were calculated as in Zhu et al. (2018). Dietary N indigestibility was based on equations published by Glover et al. (1957) for tropical grasses, and emissions were based on Waldrip et al. (2013) and Lessa et al. (2014). *Brachiaria* spp. are known to mitigate N2O emissions under field conditions (Byrnes et al., 2017), and these are known to decrease when rainfall is abundant (Fischer et al., 2016) as in the present case, and also under low soil N availability and high water filled pore space which tend to favor consumption rather than emissions 320 of N_2O (Mazzetto et al., 2014). Deducting fecal and urinary N losses from N intake allowed calculation of the N balance of growing animals. That value had to be compatible with the observed weight gains and the results were validated against Brazilian data (Valadares Filho et al., 2016) regarding N retention in relation to body size and LWGs. Methane emissions from soil were estimated based on Castaldi et al. (2006). Nitrous oxide emissions from soils have been estimated based on the summarized values from the Venezuelan savannas (Castaldi et al., 2006) and also from the values published by Copeland et al. (2012). The former authors quantified N inputs by rainfall and 328 microorganisms which amount to 2-14 kg N ha⁻¹ year⁻¹.

 The values used to estimate the above-ground and below-ground C stocks and fluxes of *B. decumbens* pastures were from contemporaneous experiments run at CRC and in close proximity to our field experiment. The methods used to determine SOC stocks in native savanna and B. *decumbens* pastures were described in Fisher et al. (1994). To estimate C footprint, we used the values of net primary productivity of savanna and *B. decumbens* pasture biomass of both above-ground (Rao et al., 1992; Fisher et al., 1998; 335 Rao, 1998; Rao et al., $2001a$; Grace et al., 2006) and below-ground (Fisher et al., 1998; 336 Rao, 1998; Urquiaga et al., 1998; Rao et al., 2001 b ; Trujillo et al., 2006). The below- ground biomass was estimated using soil coring method up to 80 cm soil depth (Rao, 1998). The C concentration in the savanna and *B. decumbens* biomass was considered as 40% and the C footprint was estimated based on: (i) CH⁴ emissions of the breeding herd including emissions from bulls (Ramírez-Restrepo et al., 2019a); (ii) CH4 and N2O emissions from animal excreta (feces and urine) embracing all animals, including the bulls (Ramírez-Restrepo et al., 2019a); and (iii) the lower and upper limits of estimated 343 C accumulation (in $CO₂$ -eq) resulting from the contribution of both shoot and root biomass into soil.

 Machinery and fertilizers were used in the establishment and maintenance (every three years) of the *B. decumbens* pastures and their CO2-eq emissions were estimated based on published reports (Edwards-Jones et al., 2009, Kim et al., 2011; University of Arkansas, 2019), and these values were prorated over time assuming the duration of the pastures as 15 years before reseeding is necessary. For the estimation of differences in overall C 350 balance between the three different animal phases, the $CO₂$ -eq GHG emissions from soil and also emissions from tillage and application of inputs to the Bd scenario were included. Emissions from tillage and application of inputs in the estimation of overall C balance of the SaBd scenario were not included.

 Data were analyzed using the general linear model procedures in SAS (2016) performing the CLM and CLPARM methods to estimate confidence limits for each 357 observation and for the parameter estimates, respectively. Effect sizes (ω^2) reported by the GLM procedure were included, and the standardized difference between important means was calculated. The model for LW (i.e. suckling and adult cattle) and LW-derived CH⁴ emissions from reproductive dynamics (i.e. birth-mating, birth-conception, gestation, calving, lactation, weaning, pre-weaning and post-weaning conceptions), and fattening period considered the fixed effects of breeding-herd grazing scenarios (i.e. Bd and SaBd) and RCs (i.e. one to six). The model for calving intervals and the conception to conception periods included RC as a fixed effect. The CORR and REG procedures were used to develop relationships for the prediction of weaning LWs from weaning age and lactation length. Least squares means (LSM) and their standard errors of the mean (SEM) were used for multiple comparisons and significant effects were declared at *P* < 368 0.05, while a tendency for significance was accepted if $P \le 0.10$.

3. Results

3.1. Animal LWs at conception, calving and weaning

 Summarized values of LWs for cows across six consecutive RCs are shown in Fig 2. 372 Liveweights at conception linearly decreased between RC1 and RC6 by 6% ($P = 0.10$; Fig 2a), while LWs at calving were similar in both RCs (Fig 2b). However, LWs over the 374 lactation period were slightly higher in RC6 (404 \pm 11.7 kg; $P = 0.10$) than in RC1 (380) 375 \pm 7.1 kg), whilst the 6% LW difference observed between both RCs (402 \pm 13.3 kg vs 376 359 \pm 8.0 kg) at weaning was significant ($P < 0.01$; Fig 2c). Liveweights during the preweaning conception stage were similar across all RCs, whereas LWs at the 378 postweaning conception stage and over the calving intervals were higher $(P < 0.05)$ in

379 RC2 (400 \pm 13.8 kg and 405 \pm 9.9 kg) than in RCs 3, 4 and 5. In suckling animals, LWs 380 at calving were significantly higher $(P < 0.001)$ in RC1 (30 \pm 0.3) than in all other RCs, but at weaning, the ~ 20 kg difference observed amongst RCs 1, 5 and 6 was not significant.

- **Fig. 2.** Mean liveweights (▼) at conception (Conc; a), calving (Calv; b) and weaning
- (Wean; c) of cows born and raised on *Brachiaria decumbens* (●) or native savanna plus
- *B. decumbens* (●) paddocks and as young heifers continuously grazed and seasonally
- mated on *B. decumbens* pastures during approximately 8.8 years.

 The mean LWs of the Bd and SaBd scenarios did not differ throughout the breeding period (Fig. 2). However, the age of females at conception, calving and weaning days was 390 significantly $(P < 0.0001)$ lower in the Bd scenario than in the SaBd scenario. This 391 difference was observed from the first RC $(28.00 \pm 1.41, 37.34 \pm 1.41, 44.96 \pm 1.54)$ 392 months vs 37.50 ± 1.41 , 46.87 ± 1.41 and 54.48 ± 1.54 months) to the sixth RC (96.26 \pm 393 2.34, 105.60 ± 2.34 and 111.56 ± 2.67 months \pm vs 105.53 ± 2.34 , 114.87 ± 2.34 and 394 121.05 ± 2.67 months).

3.2. Methane emissions and animal-environmental metrics of breeding herds

 Cumulative CH4 emissions and resulting efficiency and intensity indices during the birth-mating and birth-conception phases are shown in Table 1. In all cases, the Bd scenario had significantly (*P* < 0.0001) lower emission than the SaBd scenario, except when emissions were adjusted and compared on a yearly basis during the birth-conception phase. Beyond conventional statistical significances, the difference between means in 401 CH₄ emissions (kg heifer $^{-1}$) between birth and conception (Table 1) was large and of practical importance, at 24.17 kg (*P* = 0.95; confidence intervals 22.63-25.71). Additional birth-mating and birth-conception environmental indicators are presented in Supplementary Table 1.

 The effects of the SaBd scenario on CH⁴ emissions in reproductive and fattening- culling events of continual RCs are shown in Table 2. During gestation, emissions were significantly lower (9%, *P* < 0.0001) in RC4, while over lactation emissions in RC5 were significantly lower (17%, *P* < 0.0001) in RC4 than in RC1 Relative to the preweaning conception period in RC5, emissions in RC6 were significantly higher (63%, *P* < 0.0001), whilst the postweaning conception emissions in RC3 were significantly higher (94%, *P* < 0.0001) than in RC6. The fattening-culling routine indicated that in RC6 cows emitted 412 significantly more $(15\%, P < 0.01)$ than in RC4.

413 Overall daily CH4 emissions for cows and cow-calf pairs during the gestation and 414 lactation periods, respectively are presented in Supplementary Table 2. Daily and 415 gestation-emission ha⁻¹ values in RC1 were significantly $(P < 0.01)$ larger than the values 416 in all other RCs. When emissions were expressed in terms of AUs and AU ha⁻¹, values 417 in RC1 were similar to values in RC6, but significantly $(P < 0.001)$ lower than values in 418 the other RCs. During the lactation period, daily emissions and emissions ha⁻¹ from cow-419 calf pairs were significantly (*P* < 0.05) lower in RC2 than emissions in their RC counterparts. However, cow-calf pairs emitted larger amounts of CH₄ AU $^{-1}$ and AU ha $^{-1}$ 420 421 ^{1} in RC5 than in previous RCs.

422 Accumulated CH₄ emissions and CO₂-eq factors across successive lactations are 423 presented in Table 3. Gas emissions were significantly higher (*P* < 0.05) in the SaBd 424 scenario than in the Bd system from the first to the fourth lactation by 16%, 11%, 8% and 425 7%, respectively. Differences in the fifth $(6%)$ lactation period tended to be higher $(P =$ 426 0.10), but this effect disappeared when differences were less than 5% between scenarios. 427 Following the same pattern of decreasing differences, emitted CO_2 -eq kg⁻¹ calf born 428 tended $(P = 0.10)$ to differ between the first and fourth lactation. Throughout the study, 429 there was no difference in emitted CO_2 -eq kg⁻¹ calf weaned between scenarios, but there 430 was a tendency $(P = 0.10)$ in the second lactation.

From the first to fourth RCs, cumulative CO_2 -eq values in terms of emissions head $^{-1}$ 431 432 over the birth-gestation and birth-lactation periods were significantly higher (*P* < 0.05) in 433 the SaBd scenario than in the Bd scenario (Table 4). This significant difference was no-434 longer present in the following RCs.

 Calculated methane (CH4) emissions and derived emission efficiency indicator of commercial Brahman (*Bos indicus*) heifers born and raised on *Brachiaria decumbens* pastures or born and grown on neotropical savanna pastures until 16.4 and 25.9 months of age, respectively followed by multiple breeding phase on *B. decumbens* pastures. 440

441

442 Effect size (ω^2 : omega squared). CO₂-eq: Carbon dioxide equivalent.

443 LWG: Liveweight gain. NS: Not significant.

444

 Accumulated values of emitted CH⁴ from cow-calf pairs and derived CO2-eq indices considering calves' LW evolution during successive lactations are shown in Supplementary Table 3. Differences in emitted CH4 between scenarios decreased from the first to the last lactation by 10%, but those differences were significant (*P* < 0.05) only in four out of the six lactations. Relative to the Bd scenario, 449 the descendent order of emitted CO_2 -eq kg⁻¹ calf born in the SaBd scenario tend to be higher up to the fourth lactation, while non-significant differences were observed afterwards. Compared to the SaBd 451 scenario, emitted CO₂-eq kg⁻¹ calf weaned were significantly lower ($P < 0.05$) in the Bd scenario of the third lactation, but the values were similar in all other lactating periods. Subsequently, in all 453 episodes, CO_2 -eq kg⁻¹ calf LWG were of similar magnitude.

456 Length (days) of productive events and methane (CH₄) emissions (kg head $^{-1}$) during individual reproductive cycles (RCs) of commercial Brahman 457 (*Bos indicus*) cows born and raised on neotropical savannas until approximately 26 months of age and bred seasonally on *Brachiaria decumbens* pastures. 459

491 Methane (CH4) emissions and derived environmental efficiencies across consecutive lactations of Brahman (*Bos indicus*) cows raised and bred on 492 two contrasting systems: females born, weaned and bred full time on *B. decumbens* pastures vs females born and raised until mating on native 493 savanna followed by breeding on *B. decumbens* pastures.

494

495

496CO2-eq: Carbon dioxide equivalent. NS: Not significant.

497*P* is the probability of significance for that value between *B. decumbes* and savanna + *B. decumbes* for same variable within a same lactation period.

500 Effect of grazing *Brachiaria decumbens* pasture or neotropical savanna plus *B. decumbens* 501 pastures on cumulative carbon dioxide equivalent $(CO₂-eq)$ methane emissions across 502 consecutive reproductive cycles (RCs) of commercial Brahman (*Bos indicus*) cows. 503

504

505 NS: Not significant.

506 Within the same variable and RC, *P* is the probability of significance for a value between *B. decumbes* and

507 savanna + *B. decumbes.*

508

509 *3.3. Estimated C footprint from GHG emissions and soil C accumulation at system level*

 The estimated C footprint of GHG emissions from growing heifers grazed on either Bd or SaBd pasture scenarios, and cow-calf pairs of breeding phase and fattening phase of cull cows grazed on only Bd pastures are shown in Table 5 and Supplementary Table $\,$ 4. Total CO₂-eq enteric CH₄ emission (kg ha⁻¹ year⁻¹) from growing heifers' phase (birth-514 mating) in the Bd scenario was 927, while it was 194 in the SaBd scenario. Total CO_2 -eq 515 GHG emissions (kg ha⁻¹ year⁻¹) including CH₄ from animals, CH₄ and N₂O from feces, 516 and urinary N₂O from growing heifers' phase (birth-mating) with Bd scenario was 1,108, while it was 249 with the SaBd scenario. The duration of this phase on the Bd scenario 518 was 1.37 years, while that of SaBd scenario was 2.16 years. Total $CO₂$ -eq GHG emissions

519 from cow-calf pairs and bulls during the breeding phase (8.44 years) with Bd scenario

520 was 2,244 kg ha⁻¹ year⁻¹. Total CO₂-eq GHG emissions from the cull cows fattening

521 phase in the Bd scenario was $1,133$ kg ha⁻¹ during 0.48 years of fattening period.

522**TABLE 5**

Estimated carbon (C) footprint of greenhouse gas (GHG) emissions from growing heifers grazed on either *Brachiaria decumbens* (Bd) scenario or native savanna plus *B. decumbens* (SaBd) scenario pastures, followed by a cow-calf breeding phase and a final fattening phase of cull cows that grazed during both phases only on *B. decumbens* pastures. 527

529CH4: Methane. CO₂-eq: Carbon dioxide equivalent. N₂O: Nitrous oxide.

530**Values for fattening phase of 0.48 year.

531 Negative CO₂-eq values for soil C and C footprint imply soil C accumulation.

532The total duration of simulation in years was 10.29 for *B. decumbens* and 11.08 for savanna plus *B. decumbens* pastures. 533

534 Using the published values of above- and below-ground biomass from Bd and SaBd pastures, soil C accumulation rate was estimated to range between 1,000 to 3,000 kg ha⁻¹ 535 536 year ⁻¹ for Bd scenario which is equal to 3,667 to 11,000 CO₂-eq C accumulation and it 537 was 50 to 150 kg ha⁻¹ year ⁻¹ for SaBd scenario which is equal to 183 to 550 CO₂-eq C 538 accumulation. The CO_2 -eq emission values from soil, tillage and application of inputs 539 were included to estimate overall C footprint differences among the three phases of Bd 540 scenario. All three phases of Bd scenario showed negative C footprint values due to the 541 estimated contribution of soil C accumulation. The growing heifers' phase resulted in 542 greater negative values of soil C footprint than breeding and fattening phases. A marked 543 difference was observed in the overall C footprint between Bd and SaBd scenarios (-2,416 544 to -9,749 vs 292 to -75) for the growing heifers' phase (Table 5). SaBd scenario showed 545 a range of positive to negative CO_2 -eq values, while Bd scenario showed net removal of 546 $CO₂$ from the atmosphere.

547 **4. Discussion**

548 *4.1. Farm resources, modelling and functional C footprint during lifetime of animals*

 This study used long-term research results and dynamic modelling to predict lifetime CH⁴ emissions, animal-environmental metrics, and to estimate the mean C footprint of Brahman breeding herd systems. Growing heifers grazing neotropical savanna followed by improved *B. decumbens* pasture during the breeding life were compared with growing and mating of the females on this improved pasture, including in both cases the fattening phase of cull cows. The methodology employed provided strong evidence to support the hypothesis that the retrospective use of long-term LW data from field experiments revel differences in derived CH⁴ emissions from cattle and identifies the manner in which animal emissions, C stocks and soil C dynamics interact at system level to demonstrate $CO₂$ -eq emissions and removal from the atmosphere.

 Cows' LWs during the RCs varied within narrow ranges, and although some of the differences were statistically significant, their long-term practical significance is questionable. The same comment applies to calves' birth and weaning LWs, suggesting that there were small carry-over effects of the two different birth-mating strategies, a finding consistent with that reported by Vera et al. (2002). On the contrary, differences in age at the different reproductive events were large and persisted over the lifetime of the animals, a finding that would have important economic implications (AGROSAVIA, 2019).

 With regard to emissions, González et al. (2018) noted that 31% of Colombia's agricultural GHG emissions are accounted for by livestock, with emissions from cattle breeding systems representing 15% of the national livestock GHG inventory. González et al. (2018) indicated that there is a need to improve cattle performance to reduce emissions from breeding herds. A similar approach was followed by de Figueiredo et al. (2017) and others in Brazil to compare average production scenarios. The data on animal-environmental metrics are useful to provide an overall cattle-farming environmental picture, but this effort needs to be further complemented by *in situ* long-term measurements of animal production and CH⁴ emissions to capture the heterogeneity in herd composition, animal categories, physiological conditions, the LWs, and individual animal performance. Furthermore, there is uncertainty regarding forage intake under extensive neotropical conditions when savanna forage quality is limited, such that routine application of IPCC (2006, 2019) factors is questionable (Ku-Vera et al., 2018; Ramírez- Restrepo et al., 2019a; Ramírez-Restrepo and Vera-Infanzón, 2019). This is in agreement with Ramírez-Restrepo and Charmley (2015) and Cardoso et al. (2016) who concluded that in tropical cattle systems, data on CH⁴ emissions from pastures are scarce, and therefore the uncertainty of predictions (Ku-Vera et al., 2018) is higher than that of temperate cattle systems. There is also evidence for substantial difference between the measured values of GHG emissions from feces and urine in tropical conditions and those used from the IPCC estimates (Ruviaro et al., 2015). A detailed analysis was made in the present study using data from individual animals reveals that the differences in the overall C footprint of animals during three different phases (i.e. growing heifers, breeding and cull cows' fattening), and two scenarios (Bd and SaBd) within the growing heifers' phase. It is important to note that all three phases have negative values (gain of C or net removal of CO² from the atmosphere). The overall C footprint in the Bd scenario indicates the value of improved, conservatively managed Bd pastures for enhancing production efficiency, while reducing the environmental footprint. This was mainly due to the greater ability of Bd pastures to accumulate C in soil compared to the native savanna pastures (Fisher et al., 2007; Ramírez-Restrepo et al., 2019a). The overall C footprint of animals during the breeding phase in the Bd scenario was also negative due to net accumulation of C in soil (Fisher et al., 2007; Cardoso et al., 2016). Breeding herds are known to be responsible for a disproportionately higher share of emissions with lower production 599 values, and the breeding phase contributes much more to enteric CH₄ emission values (FAO, 2013). Thus, the strategy used in raising heifers versus breeding cows has an important effect on the productive efficiency and the C fluxes, and the data provided here allows to estimate different combinations of pasture use.

 The present study captured differential environmental burdens and structural breaks from linked beef breeding herd systems, natural and improved grasslands, and soil C fluxes as part of the ecosystem services. Recent studies from Australia [Meat and Livestock Australia (MLA), 2013; Wiedemann et al., 2015; Godde et al., 2019; Mayberry et al., 2019] and Brazil (Cerri et al., 2016; de Figuereido et al., 2017) on beef production and the environment have directed attention to system dynamics, life cycle assessments, and retrospective modelling approaches, a view reaffirmed by our analysis. The strength of this approach is that to our knowledge, we are the first to conduct in this neotropical savanna agroecosystem of Colombia an environmental study of the connection within and between the nature of Bd and SaBd beef breeding-herd dynamic systems, based on individual animal records as opposed to average herd performance (McAuliffe et al., 2018).

4.2. Methane emissions and animal-environmental metrics of breeding herds and their implications for the environment

 Overwhelming evidence was obtained from this study to show that CH4 emission outputs and tradeoffs' indicators representing different stages of production are to a large extent dynamically heterogenous (Tables 1-5). It should also be noted that across six RCs, 620 the overall cumulative cow-calf emission efficiencies in terms of kg CO₂-eq kg⁻¹ calf 621 born and t CO₂-eq year^{-1} were significantly lower in the Bd than in the SaBd herd system. The magnitude of these differences implies that robust and individual long-term records of LW in breeding herds are both needed and appropriate to examine the impact of CH⁴ emissions from animals grazing on improved tropical pastures as the model demonstrated with the use of data from savanna-based beef breeding herds (Ramírez-Restrepo et al., 2019a).

 Unfortunately, it is difficult to compare the present results with previous investigations due to differences in systems boundaries and resource uses including, but not limited, to exclusion of reared calves data (Godde et al., 2019), variable inputs, functional units and emission factors (Cerri et al., 2016; de Figuereido et al., 2017), and non-inclusion of cow-calf dynamics (McAuliffe et al., 2018) in co-production approaches (MLA, 2013). The relevance of the calculated CH⁴ yield emissions assume more significance as it indicates a relationship with the beef cattle cluster and meta-analysis of global CH4 emissions conducted by Cottle and Eckard (2018) who showed that18.48, and 635 19.56 g CH₄ kg⁻¹ DMI represent accurate emission factors from chamber measurements in Australia and tropical cattle, respectively. The CH4 yield calculated here established 637 overall cow values of 18.89, 18.30, 18.81, 18.60 and 18.70 g CH₄ kg⁻¹ DMI for gestation, lactation, conception-conception RCs, calving intervals and finishing period, respectively. The current analyses make an arguable, and conservative, simplification in that they assume that once that heifers initially raised on savanna reach mating LW they have the same reproductive performance of those raised on Bd despite the difference in age and the fact that modest negative residual effects may be expected. In fact, Vera et al. (2002) found that Brahman heifers grown at rates similar to those obtained on savanna, showed residual negative effects until the fourth gestation, while grazing on *B. decumbens* pastures.

 Drawing from the fattening period, the model reveals non-significant differences in 647 total life emissions between Bd and SaBd cows (13.344 t CO₂-eq vs 14.195 t CO₂-eq). In 648 these extremes, this implies a CH₄ energy cost of 21,842 MJ head $^{-1}$ and 23,235 MJ head 649 $^{-1}$ derived from total DMIs of 21.955 t head $^{-1}$ and 23.387 t head $^{-1}$, respectively. In other

650 words, relative to the aggregate CH₄ emitted until the second RC in Bd (6.943 t CO₂-eq) 651 and SaBd (8.023 t CO₂-eq), as cows become reproductively more efficient, the size of the 652 accumulated $CO₂$ -eq emission necessarily increases substantially up to the sixth RCs in Bd cows (35%, 50%, 54% and 59%) and SaBd cows (29%, 46%, 50%, and 54%). By contrast, there was an equilibrium between total life emissions and cow's life LWG 655 between Bd (0.030 t CO₂-eq) and SaBd (0.032 t CO₂-eq) treatments, indicating that the two systems perform very similarly over the productive life of the two herds.

 Hence, an avenue for further research is to examine the environmental implications of those emissions on carcass traits and final products in conjunction with the backgrounding and fattening of weaners and surplus heifers as proposed by Ramírez- Restrepo and Vera (2019). This discussion raises the question of whether breeders should be kept in the herd until inefficiencies (Garnsworthy, 2019) are detected or to assess their productive value as a host of environmental considerations to reduce herd sizes, and demands, on grazing, land use, and water resources. These potential alternatives and conflicts pose important challenges to farmers' decision making. These issues may lead to economic, ecological, social and natural resources vulnerability to climate change and would likely influence farmers' decisions and their variable adaptive capacity on savanna landscapes (Marshall and Smajgl, 2013; Marshall et al., 2014).

 Thus, although the aim of this study was not to derive specific guidelines for policy makers [Ministry of Environment and Sustainable Development (MINAMBIENTE), 2019], this study, based on long-term data resources, provided conclusive evidence that a sound identity for emissions from beef sources can be established, given adequate data on animal performance and its influence on the environment. Nonetheless, as pointed out earlier, the analysis performed here is representative of the global tropical beef industry. Ignoring this aspect, might lead to biased estimates in national GHG accounting [Institute

- of Hydrology, Meteorology and Environmental Studies (IDEAM), 2016)] using the IPCC
- 676 (2006) Tier 1 default factor (56 kg CH₄ head $^{-1}$ year $^{-1}$).
- *4.3. Overall C footprint at system level*

 A recent synthesis of data on grassland management impacts on soil C stocks indicated that improved grazing management, fertilization, sowing legumes and improved grass species, irrigation, and conversion from cultivation, all tend to lead to 681 increased soil C, at rates ranging from 0.105 to more than 1 t C ha⁻¹ year⁻¹ (Conant et al., 2017). Viglizzo et al. (2019) conducted a meta-analysis of published studies and they postulated that extensive grazing systems are compatible with soil C sequestration under many circumstances and that these systems can also be sustainable in various dimensions

 The present results are predicated based on pasture management practices compatible with long-term persistence and production. Pasture management is considered as a critical factor affecting GHG fluxes and C sequestration in soil in one third of the global land area under grasslands (Conant et al., 2017; Abdalla et al., 2018; Rolinski et al., 2018). Recent studies confirmed that long-term grazing experiments on reasonably well managed *Brachiaria* spp. pastures can combine high animal outputs with increasing soil C stocks in well-watered tropical areas (da Silva et al., 2017; Segnini et al., 2017; dos Santos et al., 2019). Nevertheless, Batjes (2019) cautions that best management practices are not always feasible. The present research did not address management per se. However, based on studies of Lascano and Estrada (1989) that were conducted in a similar ecosystem, this study aimed to maintain the experimental pasture in a stable, productive condition by using a somewhat more conservative approach than that recorded in the majority of farms monitored by Vera and Hoyos (2019), despite using lower fertilizer application rates than those applied by Lascano and Estrada (1989) to maintain the pastures.

 San José et al. (2014) quantified the C fluxes in the Orinoco savannas and concluded 701 that the native herbaceous vegetation is a weak C sink (36 g m⁻² year ⁻¹) in comparison 702 with *B decumbens* (216 g C m⁻² year⁻¹) pastures, whilst the soil water content influences fluxes, particularly in the native savanna. Similarly, Rondón et al. (2006) reviewed the C sequestration potential of the savannas of northern South America (20% of the 269 million ha of neotropical savannas) and also concluded that there is considerable potential for C sequestration by some deep rooted introduced tropical grasses. Implicit in these views, although the authors do not say so, is the role of adequate grassland management, that includes not only maintenance of soil cover (Fisher et al., 1998; Rao et al., 2001a; Chirinda et al., 2019), but also the need to apply low amounts of nutrients as maintenance fertilizer to sustain the growth of introduced forage species. On the contrary, the scope for increased animal production from native savannas with good management is extremely limited (Paladines and Leal, 1979).

 Sown pastures with improved grasses with deep root systems such as Bd (Saravia et al., 2014; Siqueira da Silva et al., 2019) when well-managed with proper grazing and maintenance fertilizer application can increase soil C stocks in deep soil layers up to 1 m depth while soils under poorly managed or degraded pastures may lose C compared to 717 soils under native savanna or Cerrado conditions (Fisher et al., 1994; Urquiaga et al., 1998; Boddey et al., 2010; Braz et al., 2013). Recently, dos Santos et al. (2019) confirmed the potential of two cultivars of *B. brizantha* in accumulating soil C in long-term pastures under grazing in the Atlantic forest region of Brazil. Based on the published studies on above- and below-ground net primary productivity and soil C accumulation in long-term pastures in Colombia and Brazil (Fisher et al., 2007), a range of values of annual soil C 723 accumulation of 1.0 to 3.0 t ha⁻¹ year $^{-1}$ was used for the Bd scenario to estimate the overall C footprint differences among the three phases. If soil C accumulation values are not considered for the overall C balance differences between the Bd and SaBd scenarios,

 the C footprint values will be positive for all three phases of the animals. In the estimation 727 of overall C footprint, the emissions of CH₄ from feces and N₂O from feces and urine were also included together with the values from soil, tillage and application of inputs. These additional values from soil influenced the overall C footprint of SaBd scenario (Castaldi et al., 2006) of the overall C footprint. Results from this study indicate that CH⁴ emissions from enteric fermentation is the largest proportion of total GHG emissions in different phases of Bd scenario. This observation is consistent with other published reports on beef production systems in the tropics and sub-tropics (Peters et al., 2010; Bustamante et al., 2012; de Figueiredo et al., 2017). The total GHG emissions per unit area with Bd scenario were higher than those of SaBd scenario mostly due to higher values of SR on Bd pastures. But the overall C footprint of Bd scenario was markedly more negative, while the SaBd scenario was either positive or slightly negative mainly due to greater contribution of Bd pastures through soil C accumulation. The estimation of the present C balance is conservative, and the study has avoided dealing with the biogenic C cycle in grazing systems, a topic previously debated (Adesogan et al., 2015; Wiloso et 741 al., 2016), as well as the likely short-lived effect of CH_4 (i.e. GWP₂₀ year average vs GWP100 year average; Mueller and Mueller, 2017; Allen, 2018).

 To the authors' knowledge, no systematic field experimentation has been conducted on the integration of native and sown grasslands in ranching systems. Nevertheless, Fisher et al. (1992) used a combination of on-ranch and on-station results to discuss different options and to estimate potential animal outputs, at a time when quantifying GHG emissions at a system level was still a nascent preoccupation. The present results based on long-term grazing experiments and using individual animal records, constitute a more refined initial attempt to explore some of the benefits of the complementary use of native savanna with introduced pastures in terms of GHG emissions and estimated overall C footprints.

 Extensive beef systems in the neotropical savannas characterized by low SR and low physical inputs and outputs imply relatively low pressure on the territory as exemplified by Eldesouky et al. (2018) for the Dehesa systems of Spain and Portugal. But in contrast to Dehesa systems, intensification is possible in the Llanos with the introduction of sown pastures receiving modest fertilizer inputs for establishment and maintenance. Whereas the present study, and in particular the SaBd system compared to Bd system deals with the productive efficiency and C footprint of the systems, it does not address the potential consequences of system intensification on the native savanna. As the system increases its overall SR because of the introduction of sown pastures, the savanna component may be subjected to grazing intensities that are above its carrying capacity. This is a concern expressed by Quirk (2002) and Hall et al. (2011) among others for the rangelands of northern Australia, and more generally by Reid et al. (2014), further compounded by fragmentation of the habitat, with unknown consequences (Hobbs et al., 2008).

 Intensification of rangeland utilization has been associated with a reduction in the size of ranches, and reduced variability within smaller paddocks (Ash et al., 2004). Intensification is an ongoing process in the Colombian neotropical savannas as discussed by Ramírez-Restrepo and Vera (2019) and Vera-Infanzón and Ramírez-Restrepo (2020). This process of intensification due to introduction of sown pastures and annual crops may reduce the occurrence of natural fires in the savannas with unintended consequences (CIAT-CIRAD, 2001), and it may modify energy and water balances (San-José et al., 2019). The resulting reduced biodiversity and complexity may decrease rangelands' resilience and ecosystem functions. It may also affect grazing behavior and secondary production (Hobbs et al., 2008), but these long-term trade-offs between intensification via sown pastures and possibly the reduced capacity of the surrounding savannas has seldom been investigated (Ash et al., 2004).

 The present work included different animal categories that are representative of those found in extensive beef systems, such as heifers, breeding animals, and cull cows, and showed very contrasting effects in terms of GHG emissions and overall C footprint. Their impacts on the native savanna and sown grasses were not part of the study, and the review of Rook et al. (2004) concluded that the effects of contrasting animal types on biodiversity and economic performance have been little studied. However, although the effects can be different, ideally, animal types and pasture types should be matched to increase system productivity and sustainability (Rook et al., 2004). Among others, differences in selectivity and intake between animal types may have differential effects on pasture biodiversity and persistence, while the management of these effects, together with animal welfare issues and native fauna (Hoogesteijn and Chapman, 1997; Cingolani et al., 2008), are considered important in potentially adding value to the products from extensive systems. Furthermore, systems that include several animal types and categories are inherently flexible (Astigarraga and Ingrand, 2011; Bernués et al., 2011) and therefore, more resilient, and losses and gains in sustainability can be offset by combining different animal categories (Stackhouse-Lawson et al., 2012). Inevitably, there may be trade-offs between efficiency of production per hectare and environmental impacts in year-round grazing schemes (Casey and Holden, 2006; Ridoutt et al., 2011; Snow et al., 2014), and data such as presented here may contribute to understand their functioning in a tropical setting.

5. Conclusions

 This study predicted CH⁴ emissions, animal-environmental metrics and C footprint over the productive lifetime of the tropical beef cattle herds by: (i) comparing the common strategy of raising replacement heifers on native savanna up until reaching mating LW followed by breeding on improved *B. decumbens* pasture; and (ii) exploring the

 environmental implications of fattening the resulting cull cows using *B. decumbens* pastures. Major lessons learned from this study include: (i) CH⁴ emissions from Brahman breeding herds are lower than emission estimations from IPCC; (ii) animal production phases (i.e. growing heifers, cow-calf-bull, cull cows) influence GHG emissions and C balance within a beef production system; and (iii) well-managed, grazed *B. decumbens* pastures management contribute to net C gain through soil C accumulation. Furthermore, multi-year individual records allowed the identification and quantification of trade-offs at the system level, and suggested further hypothesis regarding the interplay of the environment, biological efficiency, reproductive performance, GHG emissions and farming management.

 Future research should address the persistence and resilience of the remaining native neotropical savannas in production schemes that will inevitably not only increase the systems' grazing pressure, but also generate new trade-offs in terms of animal production and the environment. As shown in the present work, the impact on GHG emission and C balance from production strategies regarding replacement heifers, the breeding herd and the disposal of cull cows is sensitive to the particular combination of subsystems chosen.

Acknowledgments

 Authors would like to thank the former Tropical Pastures Program at the International Center for Tropical Agriculture (CIAT) and Carimagua Research Center (CRC) for core 821 funding to sustain field experiments and to provide technical assistance. The on-station herd experiment was designed by R.R Vera-Infanzón and implemented by him and C.A. Ramírez-Restrepo. We wish to thank the Commonwealth Scientific and Industrial Research Organization (CSIRO) for the time provided to the senior author to collate initial datasets, while working there. The improved dynamic simulation model, meticulous data 826 analysis and interpretation, and manuscript preparation activities from 2017 to 2020 were

- carried out by the authors supported by resources and time provided by current
- 828 professional practices. Lastly, the authors are very grateful for the suggestions received
- 829 from an anonymous reviewer that improved significantly the quality of the manuscript.

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