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Contribution of dung beetles to cattle productivity in the tropics: A stochastic-dynamic modeling approach

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ABSTRACT

Dung beetles provide different services to agroecosystems. Previous economic assessment of this insect group highlights their importance in temperate zones using linear models or ecosystem services frameworks. This paper proposes a stochastic-dynamic model to simulate dung production and degradation in order to estimate the contribution of dung beetles to dual-purpose cattle production in the tropical grasslands of Veracruz, Mexico. The model allowed for estimation of sampling distributions of dung occurrence in the field, the coverage area, nitrogen burial, and maintenance of clean grasslands and their economic benefits. Contributions of dung beetles are expressed as 95% confidence intervals. Dung beetles removed from 56.2 to 116.9 depositions $ha^{-1} d^{-1}$ and the efficiency in dung removal was between 65 to 69%. At the grassland scale, dung beetles cleaned an area from 8.5 to 26.9 $m^2 ha^{-1} d^{-1}$. Nitrogen burial ranged from 32.2 to 136.2 $kg ha^{-1} y^{-1}$. The clean area maintained annually varied between 31 to 98% of the pastures. The annual benefit per animal unit ranged between US $149.1 to US$ 423.6 and at state level the benefit (US$ × 10E6) was between 140.6 and 455.8. The most important economic contribution was maintaining clean areas (71.4%), then by incorporating nitrogen as fertilizer (28.3%), and last in milk and meat benefits (< 1%). The model allowed for the representation of the natural variability of some key factors involved in dung processing by beetles related to dual-purpose cattle production.

1. Introduction

Dung beetles perform different roles in natural and agricultural systems by participating in seed dispersal, nutrient cycling, and parasite reduction (Nichols et al., 2008). Some of these activities benefit humans and are considered as ecosystem services (Millenium Ecosystem Assessment, 2005). The benefits provided by dung beetles depends on the species richness and abundance in a given area (Manning et al., 2016), but some human activities affect their populations, such as the use of some parasiticides which can reduce dung beetle populations (Beynon et al., 2012). Dung burial by coprophagous beetles has long been recognized as a positive activity in agricultural production (Boyd and Banzhaf, 2007). In the United States, the economic value of dung beetles was calculated first by Fincher (1981), and then by Losey and Vaughan (2006); its economic contribution was estimated at US$ 380 million, composed of different services. A recent paper reported the economic benefits of dung beetles in the United Kingdom (Beynon et al., 2015), where their estimated contribution was almost US$ 560 million per year. In addition to the reduction in costs by dung beetle activities, there are costs incurred when restoring dung burial services, related to research activities and programs aimed at introducing these insects into areas where they are not present, for example in Australia (Edwards, 2007).

The value of dung beetle activity has been estimated by computing the difference between the costs of services when the beetles are present and when they are absent (Losey and Vaughan, 2006), that is, equating beetle activities to alternate services for generating benefits. The difference is computed for each of the services the beetles provide and the total is the sum of all savings. This method has also been applied to compute the economic value of biological control agents (Cullen et al., 2008). The approach is based on point estimates, which generate unique values, but the natural variability of the different processes is not taken into account. In contrast, stochastic models simulate the input variables as observations sampled from probability

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distributions, and then processing them in the required sequence to obtain a distribution of the response variable (Burmaster and Anderson, 1994). Therefore, this approach allows representing and measuring the natural variability of the target process (Atanassov and Dimov, 2008). Stochastic simulation has been employed to evaluate the economic impact of non-native nocive species in Southeast Asia (Nghiem et al., 2013), fault tree analysis of spittlebug occurrence (García-García et al., 2006), and microbiological risk assessment (Peleg et al., 2007). Likewise, dung production and decay is a dynamic, complex process (Laing et al., 2003; Hirooka, 2010), and is a key element for modeling the contribution of dung beetles to cattle productivity; hence the necessity to consider both the inherent variability and the dynamics of the processes involved.

While the previous studies of dung beetle economic contributions help to recognize their importance, these works have been carried out in temperate zones with certain cattle breeds and using deterministic, *ad-hoc* models or frameworks. Therefore, dung beetle contribution may be different with other cattle types or production systems like those implemented in tropical regions (Slade et al., 2016). The state of Veracruz, Mexico, contributed 464,980 tons of meat and 706,981 m^3 of milk in 2013, ranking it in first and sixth place, respectively (SIAP, 2015a). The state has a cattle population of about 3.7 million head, and ranch area near to 3.7 million ha, covering > 50% of state land (SIAP, 2015b). Unlike other production systems in central and northern states of Mexico, most of the cattle are managed on grasslands and pastures, and few are confined. Cattle are dual-purpose, producing milk and meat, a common practice in tropical cattle production systems (Vilaboa and Díaz, 2009). In addition, their productivity is low due to inefficient management practices and race adaptability (Vilaboa et al., 2009). Dung beetles are important components of cattle production systems in Veracruz; nearly 60 species contribute to the degradation of dung produced by cattle, horses and other vertebrates in pastures and forests (Halffter and Edmonds, 1982), and communities between 11 to 15 species are present in the tropical grasslands most of the year (Montes de Oca, 2001; Flota-Bañuelos et al., 2012; Martínez and Suárez, 2012). Their effect on dung degradation fluctuates during the year, with the highest decomposition rates occurring during the rainy season (Cruz et al., 2012). Due to the impact of dung beetle activity on agroecosystems, the relevance of cattle production in Veracruz, and the intrinsic variability of these factors, the purpose of this research was to assess the contribution of this insect group to cattle productivity using a stochastic-dynamic modeling approach.

2. Materials and methods

2.1. Description of the dung pat stochastic-dynamic model

The conceptual model of cattle deposition dynamics, as affected by dung beetle activity is presented in Fig. 1. It is assumed that under current management practices, a cattle population (*Ht*) is raised on a delimited pasture area (*At*), the height of the rectangle in Fig. 1. In tropical regions, cattle are maintained in the field throughout the year (Diaz-Rivera et al., 2011), thus, at any time, cattle are producing dung pats, which in turn are decomposing at a certain rate, and reach an equilibrium in the area covered. The presence of dung beetles accelerates dung decay compared to when no dung beetles occur in the field. Thus, the area covered with dung pats is smaller due to dung beetle decomposition activities (Cruz et al., 2012). In Fig. 1, the area covered with dung pats when beetles are active is *Ab*, while the area covered when beetles are not present is $Au = Ab + Ac$, thus *Ac* is the area cleaned by the dung beetles. The area covered by dung pats fluctuates during the year because of changes in the effectiveness of dung removal between the dry and rainy seasons (Cruz et al., 2012). The clean area supports a cattle population (*Hc*), which is a fraction (*Ac*/*At*) of population *Ht* and represents the direct contribution of dung beetles to productivity, expressed as the proportion of milk and meat production.

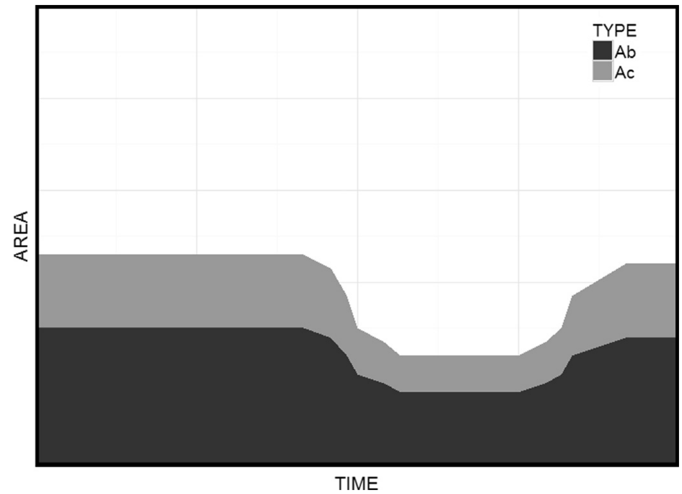

Fig. 1. Graphic representation of the dynamics of a grazing area covered by dung pats over time and the effect of dung beetles. The height of rectangle represents the total surface area (*At*) on which a given number of cattle (*Ht*) are managed; *Ac* is the area cleaned by dung beetles and *Ab* is the area which is always fouled because of the constant production of dung by cattle.

The indirect contribution of dung beetles is by the constant cleaning of the grazing area and by increasing the amount of nitrogen incorporated to the soil from burial activity. In this model, we assume that productivity derives basically from the grassland as the main forage source for cattle (van der Linden et al., 2015).

2.2. Stochastic-dynamic modeling approach

In this model, it is assumed that parasiticides are not applied to cattle because dung beetles are negatively affected by these products (Sommer and Bibby, 2002; Beynon et al., 2012). Therefore, *Ht* is the target cattle population not subject to parasiticide applications and it was computed as:

$$Ht = H*Pt \tag{1}$$

where *H* represents the total number of non-confined cattle existing in the state of Veracruz in a given year, and *Pt* is the proportion of cattle not subject to parasiticide applications. Moreover, *At* is the area occupied by the *Ht* population and is proportional to all of the grazing area in the state (*A*):

$$At = A*Pt \tag{2}$$

The dynamics of dung occurrence under field conditions is a complex process which basically depends on cattle deposition and decomposition rates. Dung pat occurrence under field conditions was modeled as a first order differential equation:

$$d(Ej)/dt = Kp*AU - rj*Ej \tag{3}$$

Eq. (3) represents the dynamics of dung pat abundance per day (*Ej*), as a function of total depositions minus dung removal, *j* indicates if dung beetles are present (*b*) or absent (*u*). *Kp* is the number of depositions per cow per day. Individual cattle were converted to animal units (*AU*), where one *AU* equates to a 450 kg cow (Teixeira et al., 2012); *AU* were used to standardize the different age classes of cattle. The term *rj* is a decomposition parameter of a first order exponential decay model, representing dung breakdown (Sommer and Bibby, 2002; Cruz et al., 2012). The value of *Ej* was solved from Eq. (3) for the steady state, that is, when $d(Ej)/dt = 0$, resulting in the following equation:

$$E_j = Kp*AU*r_j^{-1} \tag{4}$$

The degradation rates (*rj*) were estimated by fitting an exponential nonlinear regression model to data obtained from field-level experiments involving the activities of a community of dung beetle species for the dry and rainy seasons in Veracruz (Cruz et al., 2012). The most common species in the rainy season were *Euoniticellus intermedius*, *Digitonthophagus gazella*, *Copris lugubris*, and *Haroldiellus sallei*, while in the dry season the active species were *E. intermedius*, *D. gazella*, and *Labarrus pseudolividus*, these species are the most abundant in central Veracruz (Flota-Bañuelos et al., 2012). Dung pats removed by beetles (*Ec*) were computed as the sum of the differences in pat production, weighted by the dry and rainy season duration:

$$Ec = a(E_u - E_b) + (1 - a)(E_u - E_b) \quad (5)$$

where a is the fraction of the year corresponding to the dry season and (1-a) is the proportion of the rainy season.

The target cattle population was converted to *AU* using the equation:

$$AUt = Ht*AUw \quad (6)$$

where *AUw* is the equivalent *AU* value of each cattle individual, estimated as a weighted average:

$$AUw = 450^{-0.75}\sum_i qi*Wi^{0.75} \quad (7)$$

where *qi* is the proportion of cattle in age class *i* related to the whole statewide population, *Wi* is the live weight of cattle in age class *i*, and the exponent 0.75 is an empirical coefficient to adjust the metabolic weight (García-Peniche and Lopez-Guerrero, 2015); age classes were: cow, calf, heifer, bull, and steer.

The dung pats cover a surface (Omaliko, 1981), therefore, the dung removed (*Ec*) was transformed to clean pasture area (*Ac*), from which the number of *AUc* that can be supported was derived. The clean pasture area generated by the dung beetle activity is:

$$Ac = Ec*Af \quad (8)$$

where *Af* is the area fouled by dung pats and is larger than the physical dung-covered surface because cattle avoid eating in areas containing the fouled grass (Teixeira et al., 2012).

The cattle raised in the clean area (*AUc*) is proportional to the target cattle population density and corresponds to the direct contribution of dung beetles to cattle productivity:

$$AUc = Ac(AUt\ At^{-1}) \quad (9)$$

The benefit to milk (*Vm*) from cows supported by the clean area was computed as:

$$Vm = Pm*AUc*(M\ AU^{-1}) \quad (10)$$

where *Pm* is the price of milk, and *M* is the annual milk production by the total cattle population (*AU*), in the statewide productive area *A*; thus, $M * AU^{-1}$ is the milk productivity per animal unit. *AU* was computed with Eq. 6 using the total cattle population (*H*).

In the same way, the value of meat (*Vg*) was calculated as:

$$Vg = Pg*AUc*(G\ AU^{-1}) \quad (11)$$

where *Pg* is the price of meat, and *G* is the annual meat production by the total cattle population.

On the other hand, the indirect benefits were computed based on the total nitrogen buried and the daily maintenance of the clean area during an entire year. Therefore, because it is assumed that dung beetles are always active, the total clean area is the accumulation of the daily clean area (*Ac*) during a year and its value (*Vc*) is:

$$Vc = 365*Pc*Ac \quad (12)$$

where *Pc* is the alternate cleaning cost per unit area instead of the cleaning service provided by dung beetles.

In the case of nitrogen, its benefit was computed as its value as fertilizer; the buried nitrogen has an economic value (*Vn*) computed as:

$$Vn = 365*Pn*Kn*Ke*Kf*Wd*Ec \quad (13)$$

where *Pn* is the price of nitrogen fertilizer, *Kn* is a coefficient representing the proportion of nitrogen contained in the dry dung pats, *Ke* is a conversion coefficient from fresh to dry content, *Kf* is an efficiency coefficient because dung burial does not occur instantly leading to partial nitrogen loss, *Wd* is the weight of fresh pats, and *Ec* as defined before. The efficiency coefficient (*Kf*) was computed as 1-(*rb*/*ru*), the reduction in the decomposition mean time (1/*r*) when dung beetles are present.

The total economic benefit provided by dung beetles for the state of Veracruz was computed as the sum of savings for the different services evaluated (*Vi*), and all the monetary values were adjusted for inflation to year 2013 and converted to US dollars at the conversion rate for that year: US$ 1 = MX$ 13.08. In this model, parasite and fly control was not accounted for to avoid duplication in cost expenditures; by considering dung cleaning with Eq. (12), we assumed that cleaning removes the dung (Fig. 1), thus eliminating the source for parasites and flies and no additional control measures were required.

2.3. Probability model selection and parameter estimation

In the previous equations, upper-case letters correspond to random variables and lower-case letters refer to constant coefficients; thus, stochastic variables were sampled from probability distribution models or by bootstrap sampling (Clemen and Winkler, 1999; Vose, 2008). The constants and model parameters were estimated from production statistics, published data, or expert opinion. The stochastic values from the distributions were generated using Latin Hypercube Random Sampling, which is a form of stratified sampling that allows a better representation of the variable distribution shape (McKay et al., 1979); samples were extracted with a size of $n = 50{,}000$. Descriptive statistics were computed at dung pat, grassland, or state-wide levels as required, and variability was estimated by computing a 95% confidence interval at 0.025 and 0.975 percentiles from the samples. The computations were performed with Mathematica v8.1 (Wolfram Research, 2010) and R v3.2.2 (R Core Team, 2015). Figures were created by using the grammar for graphics instructions (Wickham, 2010).

3. Results and discussion

3.1. Cattle population and dung production model components

Parameters and distribution models to estimate the number of cattle (*Ht*) receiving dung beetle benefits, and dung production are presented in Table 1, while the models and parameters used to compute the animal unit equivalents (*AU*) are provided in Table 2. Most of the parameters were retrieved from published data and the proportion of non-deparasitized cattle and dry season duration were estimated by experts. We applied bootstrap sampling to production statistics and the Pert distribution to variables for which we obtained extreme and most probable values.

The analysis indicated that the state target population ($AUt \times$ 0E6) had a mean = 1.007, SD = 0.136, and 95% CI (0.757, 1.270), corresponding to nearly 30% of the total non-confined state cattle population (sampling distribution in Fig. 2). This population was raised within 1.109 (× 10E6 ha), SD = 0.139, 95% CI (0.847, 1.370). In the case of cattle density, most of it was below one $AUt\,\text{ha}^{-1}$ (Fig. 2), with a mean = 0.908, SD = 0.046, and 95% CI (0.823, 0.991). Dual-purpose cattle production systems are common in tropical regions of Mexico (Rojo-Rubio et al., 2009) and produce milk and meat, but most of the cattle producers are in the low technology, low resource input category, and therefore contribute fewer numbers to the estimated animal density per hectare (Vilaboa et al., 2009).

In general, the estimated animal density agrees with previous reports for the state of Veracruz. Diaz-Rivera et al. (2011) found that 80% of dual-purpose cattle are managed using low input technologies in Las Choapas, the municipality of Veracruz with the largest number of cattle. They found an average of 1.3 $AU\,\text{ha}^{-1}$ (± 0.5 SE) across all the

Table 1
Constants, model parameters and distribution models related to the estimation of cattle receiving dung beetle benefits, and dung production.

Variables (units)	Constants and distribution model (parameters)	Source
H (individual cattle)	Sample (4020544, 4043398, 4049673, 4051673, 3622995, 3781199, 3866149, 3902925, 3714244, 3785073)[a]	SIAP (2015b)
A (ha)	Sample (3684089, 3684089, 3684089, 3684089, 3692167, 3680888, 3689412, 3718994, 3757487, 3696773)	INEGI (2015)
Pt (proportion)	Pert (0.2, 0.3, 0.4)[b]	Expert opinion
Kp (deposition AU^{-1} d^{-1})	Pert (2, 12, 16)	Omaliko, 1981; Hirata et al., 2011; Teixeira et al., 2012
rj (d^{-1})	*rb* = 0.1687, *ru* = 0.0632 for dry season; *rb* = 0.4534, *ru* = 0.1056 for rainy season	Cruz et al., 2012
a (proportion)	*a* = 0.6	Expert opinion
Af (m^2 deposition^{-1})	Pert (0.08, 0.191, 0.301)	Castle and MacDaid, 1972; Omaliko, 1981; Teixeira et al., 2012

[a] Bootstrap sample parameters are statistics from years 2004 to 2013.
[b] Pert parameters correspond to minimum, most probable, and maximum, respectively.

Table 2
Constants, model parameters, and distribution models used to estimate animal unit equivalents (*AUw*).

Cattle age class *i*	Distribution model and parameters for live weight (*Wi*) (kg individual^{-1})[a,c]	Proportion of age class (*qi*) in the state population[b]
Cow	Pert (377, 440, 502)	0.5590
Calf	Pert (163, 230, 284)	0.2683
Heifer	Pert (245, 331, 416)	0.1239
Bull	Pert (561, 700, 783)	0.0253
Steer	Pert (300, 400, 470)	0.0233

[a] Source: Vilaboa and Díaz (2009).
[b] Source: PGN (2015).
[c] Pert parameters correspond to minimum, most probable, and maximum, respectively.

production systems, and they reported that only 3% of the producers are business-oriented. Moreover, in central Veracruz, between 93.6% and 95.5% of cattle producers fell into the low input category (Vilaboa and Díaz, 2009; Vilaboa et al., 2009).

3.2. Dung production dynamics

The temporal dynamics of daily dung occurrence per hectare during a given year is displayed in Fig. 3, which shows the stochastic, numerical solution of Eqs. (4) and (5). The figure presents seasonal variation: high numbers of dung pats at the beginning of the year followed by a decline during the rainy season (June to September, Julian days 151 to 296), and then an increase reflecting the differences in the degradation rates between the dry and rainy seasons. According to the model, there are always dung pats present in the field, but their number is higher when no dung beetles are present; decomposition rates also are higher during the rainy season (*rb* in Table 1), thus reducing dung occurrence. Dung pat deposition (*Eb*) (ha^{-1} d^{-1}) were: mean = 44.3, SD = 8.7, 95% CI (26.3, 59.6), while for dung removed (*Ec*) was: mean = 88.3, SD = 15.8, 95% CI (56.2, 116.9). It is clear from the figure that the low and high percentile values derive from the rainy and dry seasons, respectively. The effectiveness in dung reduction by beetles had a mean value of 66.6% with a 95% CI (64.7, 69.0). These results reflect what is known about the population ecology of these insects in the tropics: a greater abundance during summer (rainy season) and lower abundance during winter (dry season) (Flota-Bañuelos et al., 2012; Martínez and Suárez, 2012), and a more rapid dung degradation during the rainy season (Cruz et al., 2012). Although

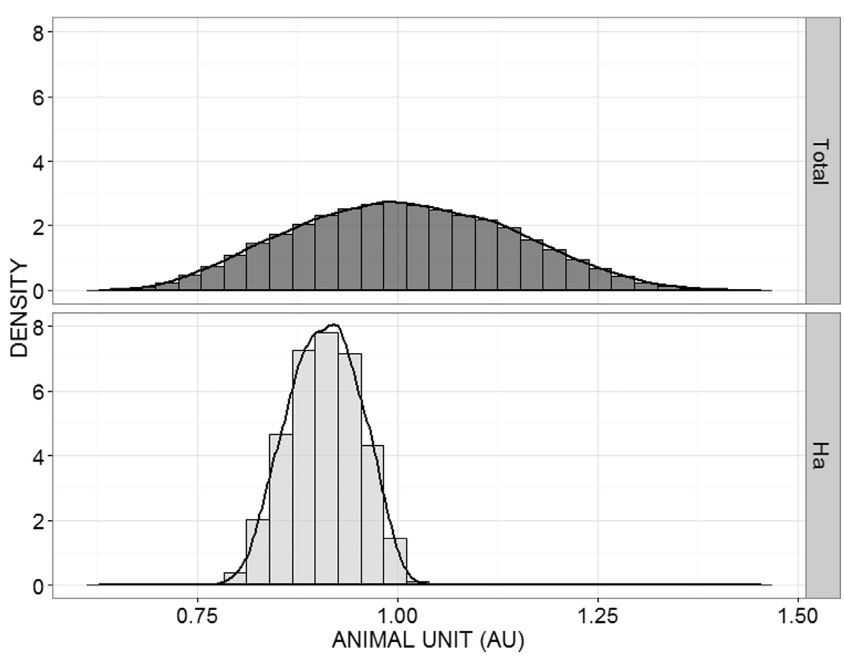

Fig. 2. Sampling distributions of non-treated, dual-purpose cattle population in Veracruz expressed as animal units (*AU*) (Total, *AUt* × 10E06), and animal density per hectare (Ha, AU_t ha^{-1}).

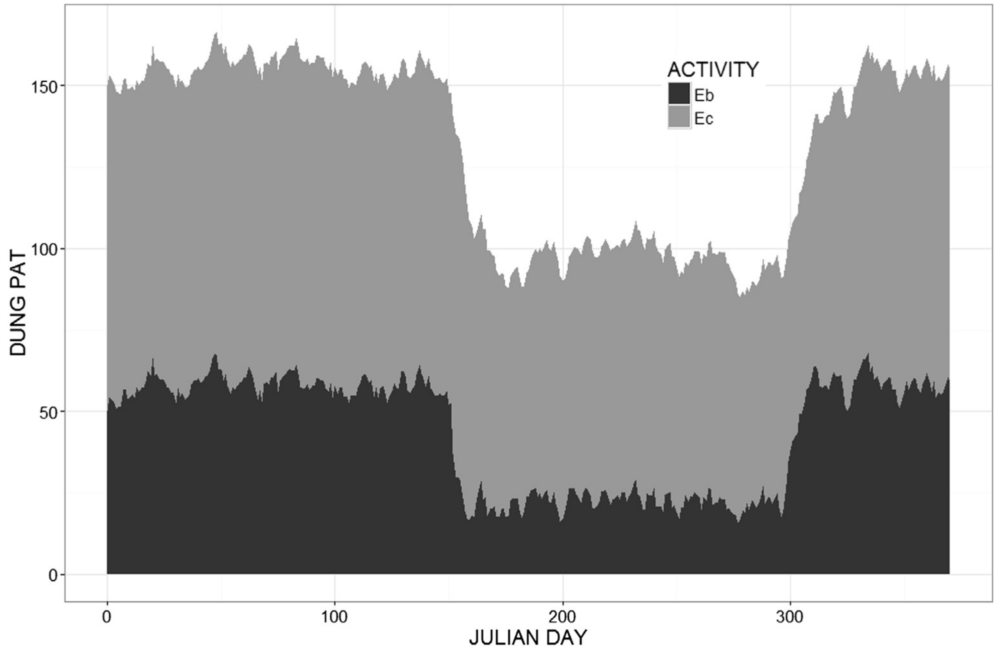

Fig. 3. Daily dung pat presence per hectare when dung beetles are present (*Eb*), and dung pats removed by beetles (*Ec*). The upper border represents the dung pat occurrence when no beetles are present.

our model simulates the daily and dry-rainy seasonal dung dynamics, dung beetle populations fluctuate across all seasons (Flota-Bañuelos et al., 2012) and across years (Escobar et al., 2008). Thus, long-term data and other model components are required to better understand how other factors, like climate change and land use affect species diversity, abundance and effectiveness of dung degradation by beetles (Escobar et al., 2008; Dortel et al., 2013) as continuous grazing usually reduce arthropod diversity (Van Klink et al., 2015). On the other hand, the number of dung pats occurring during a day was higher than the number of daily depositions by cows (*Kp*) (Table 1), because dung degradation is a delayed process which makes dung pats accumulate over time until a steady state is reached. These findings agree with previous reports highlighting the time delay in dung pat decomposition (Madsen et al., 1990; Dimander et al., 2003).

Dung pats occupy an area where the grass is not palatable to cattle (Stockdale and King, 1983). The area always fouled by dung (*Ab*) and the cleaned areas (*Ac*) are presented in Fig. 4. The statistics for *Ab* were ($m^2\ ha^{-1}\ d^{-1}$): mean = 8.4, SD = 2.5, 95% CI (4.1, 13.7), and for *Ac*: mean = 16.8, SD = 4.8, 95% CI (8.5, 26.9). The average clean area comprises 0.17% of a hectare; therefore, the direct contribution of dung beetles to productivity is very limited. On the other hand, the daily dung removed by beetles during an entire year corresponded to a total clean area (× 10E6 ha) with a mean = 0.682, SD = 0.214, 95% CI (0.325, 1.151). This area is equivalent to 61.5%, SD = 17.5, 95% CI (31, 98.1) of the state grazing area (*At*) where the target cattle are raised and is the indirect contribution of dung beetles to dual-purpose cattle productivity as a cleaning service; this service works better when species diversity increases (Slade et al., 2007; Tixier et al., 2015; Manning et al., 2016).

The statistics of the area covered by dung pats obtained in the present report are slightly higher than those reported by Teixeira et al. (2012). They computed fouled areas ranging from 1.2 to $3.6\ m^2\ ha^{-1}\ d^{-1}$ using a simple multiplicative model with *AU* densities varying between 1.9 and 4.3 $AU\ ha^{-1}$, but without assuming a decomposition delay. Moreover, results obtained by Omaliko (1981) indicated that dung pats cover between 0.02 to 0.05% of the grazing area in the savannas of Nigeria, smaller values than those reported here. On the contrary, in temperate grasslands, the fouled area reported by Beynon et al. (2015) was 4.8%, while Slade et al. (2016) reported a value of 4% in Finland, and suggested that in tropical regions the decomposition rates should be higher. In our research, we estimated that the mean lifetime of dung pats ($1/r$) varied from 2.2 to 5.9 d when dung beetles are present while for rangelands in California the mean time was 22.7 months (Losey and Vaughan, 2006). Also, we found a dung reduction of 66.6% as compared to 19.1% by Losey and Vaughan (2006) which contrasted with the reduction values ranging from 4.4% to 31.7% reported by Beynon et al. (2015). Therefore, our results confirm that in tropical regions dung decomposition is faster than in temperate zones and this may be due to a higher diversity of dung beetle species, a larger body size and year-round presence (Kohlmann, 1991; Flota-Bañuelos et al., 2012; Nervo et al., 2014). It is interesting to note that our method was able to measure the daily, fluctuating between-season contribution of dung beetles to keep the pastures less fouled than if they were not present. This small surface area, when accumulated over an entire year, represented at least 31% of the target grazing area and reached almost 100% in the best case scenario.

3.3. Economic value of dung beetle services

The models and parameters used to compute the economic contribution of dung beetles are presented in Table 3. Again, we were able to obtain measured parameters for most of the distributions; only for the machinery cleaning service and the fresh dung pat weight did we consult experts to estimate their variability. Under current management practices, we computed a meat productivity of 134.6 $kg\ AU^{-1}\ ha^{-1}\ y^{-1}$, SD = 13.0, 95% CI (109.2, 158.5), with a value of US$ 222.9, SD = 22.6, 95% CI (179.1, 264.8); meaning that 1 ha supports a cow that produces a calf in a little more than one year (Vilaboa et al., 2009). The proportional meat production due to the cleaned area by dung beetles was 0.2 $kg\ AU^{-1}\ ha^{-1}\ y^{-1}$, SD = 0.06, 95% CI (0.1, 0.3), which contributes US$ 0.34, SD = 0.1, 95% CI (0.15, 0.56), a value less than one dollar per hectare per year. In the case of milk, the productivity was 209 $L\ AU^{-1}\ ha^{-1}\ y^{-1}$, SD = 11.3, 95% CI (189, 232.2), with a value of US$ 79, SD = 8.1, 95% CI (62.7, 93.3). The savings due to dung beetles corresponded to 0.32 $L\ AU^{-1}\ ha^{-1}\ y^{-1}$, SD = 0.1, 95% CI (0.16, 0.51) and its value was US$ 0.12, SD = 0.04, 95% CI (0.06, 0.2), again this is less than one dollar per hectare per year.

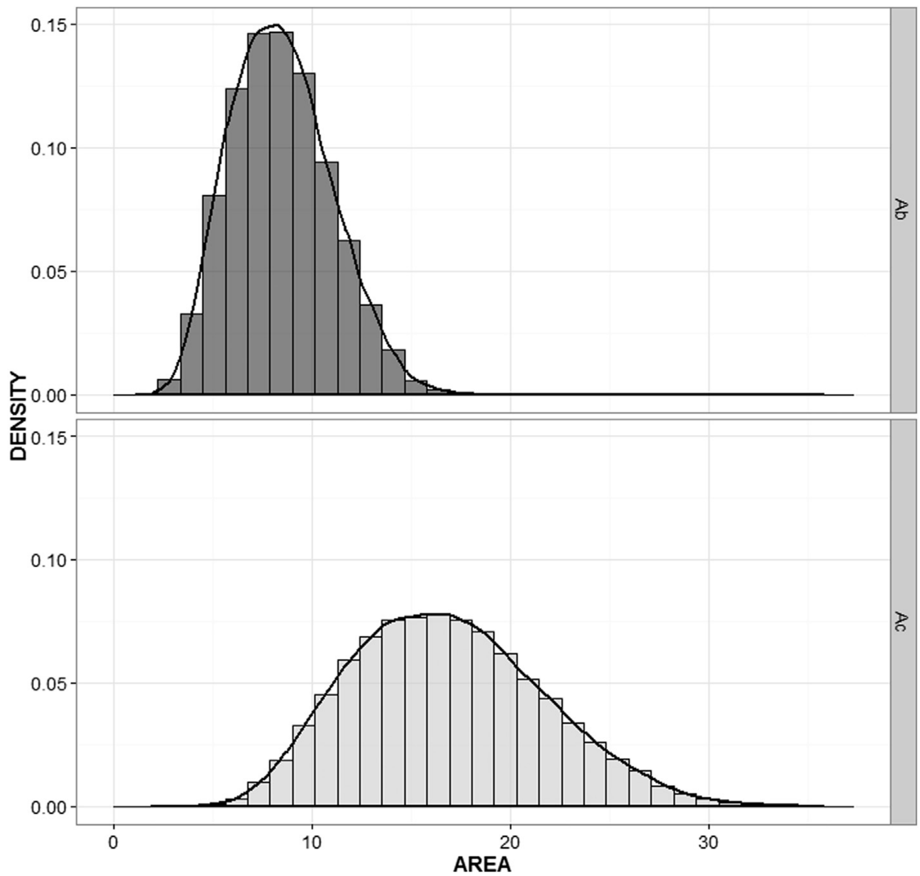

Fig. 4. Sampling distributions of area ($m^2\ ha^{-1}\ d^{-1}$) covered by dung (*Ab*) and area cleaned by dung beetle activity (*Ac*).

The annual value of the direct contribution of dung beetles to cattle productivity is shown in Fig. 5 for milk and meat at the state level. Profit statistics (US$ × 10E6) for milk values were: mean = 0.133, SD = 0.043, 95% CI (0.062, 0.231), while meat profit (US$ × 10E6) values were: mean = 0.377, SD = 0.123, 95% CI (0.175, 0.654). On average, meat profit was almost three times the milk profit and meat profit was more dispersed than milk profit. This contribution is referred to as forage fouling by Losey and Vaughan (2006) and its effect has been measured on meat value only; here, we emphasize the dual-purpose nature of cattle production and compute both meat and milk benefits.

The estimates of dung dynamics and grassland area cleaned by dung beetles indicate that while dung beetle effectiveness in reducing dung is 66.6%, this reduction only translates into a modest contribution on a per unit area because dung pats cover only a very limited productive surface due to the fast degradation rates. Pasture fouling was valued as a land tenure cost by Beynon et al. (2015), but here we considered the grassland surface as the source of cattle productivity, following an input-based conceptual model (van der Linden et al., 2015). That is, we considered that cattle production essentially depends on the grassland productive area, particularly of the forage species present, their nutritive value and their management (Lascano, 2002; Absalón-Medina et al., 2012), and that any reduction of it will diminish the production of milk and meat. Nonetheless, it is possible to increase this contribution if better management practices are implemented, for example, by including trees and forage shrubs, or by planting good quality grass and legume forages (Absalón-Medina et al., 2012; Montoya-Molina et al., 2016). Moreover, our findings have the same

Table 3
Constants, model parameters and distribution models used to estimate the value of milk, meat, nitrogen and clean area derived from dung beetle activities.

Variables (units)	Constants and distribution model (parameters)	Source
Pm (US$ ML^{-1})	Sample (367.3, 372.6, 312.6, 340.3, 353.7, 392.6, 413.2, 406.9, 411.9, 405.9)[a]	SIAP (2015c)
M (ML)	Sample (687691, 683046, 681809, 692754, 683203, 708230, 722465, 723106, 715190, 706981)[a]	SIAP (2015c)
Pg (US$ Mg^{-1})	Sample (161.1, 169.1, 168.4, 164.2, 170.8, 168.3, 163.4, 153.9, 165.2, 171.6)[a]	SIAP (2015c)
G (Mg)	Sample (381930, 399873, 429691, 437064, 453339, 465483, 496438, 502508, 481098, 464980)[a]	SIAP (2015c)
Pc (US$ ha^{-1})	Pert (259.45, 288.28, 324.32)[b]	Expert opinion
Pn (US$ Mg^{-1})	Sample (875.526, 803.226, 767.902, 979.321, 971.542, 929.269, 912.288,1234.66, 1209.98, 927.403)	(SNIIM, 2015)
Kn (proportion)	Pert (0.015, 0.02, 0.023)	Teixeira et al., 2012
Ke (proportion)	Pert (0.159, 0.18, 0.20)	Gonzalez-Avalos and Ruiz-Suarez, 2001; Li et al., 2012
Kf (proportion)	Pert (0.62, 0.69, 0.76)	Cruz et al., 2012
Wd (kg $deposition^{-1}$)	Pert (0.4, 0.8, 2)	Expert opinion

[a] Bootstrap sample parameters are statistics from years 2004 to 2013.
[b] Values correspond to minimum, most probable, and maximum respectively.

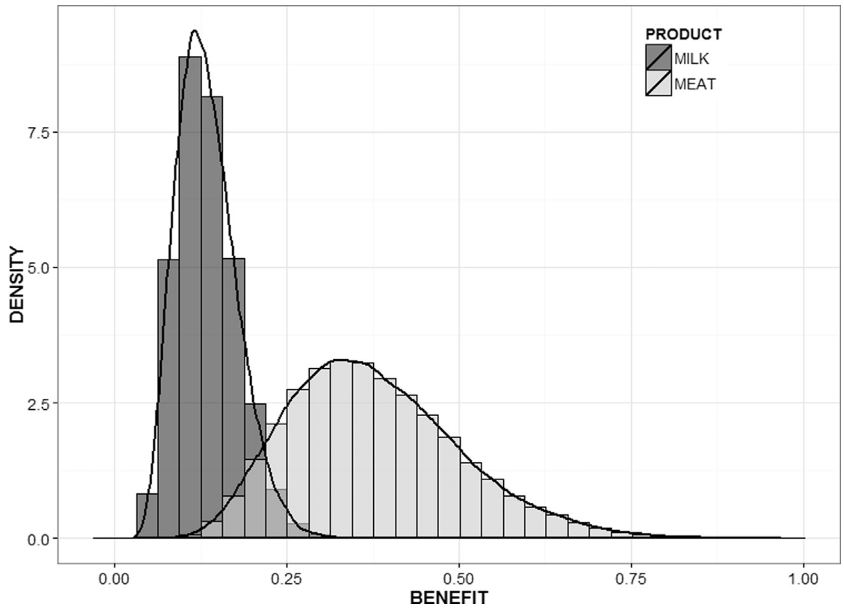

Fig. 5. Sampling distributions of the annual direct benefit of dung beetle activities to dual-purpose cattle productivity at the state level, expressed as value for milk and meat (US $ × 10E6).

decreasing pattern as those reported by Slade et al. (2016) regarding the scale of assessment; that is, at the dung pat scale we found a high effectiveness (66.6%), but at the grassland level the effectiveness is only 0.17% because dung pats cover a small fraction of the productive area, regardless of dung beetle occurrence.

Our results contrast with those published by Losey and Vaughan (2006). For meat, they found a savings of 6.2 kg per animal per year. As we have shown, dung decomposition is slower in temperate and cold zones than in tropical zones so the proportion of fouled pasture increases; in fact, as mentioned before, it has been reported that nearly 4% of grasslands are covered by dung in cold zones (Slade et al., 2016), so meat loss could be higher. Moreover, our model indicates that because dung production is continuous and decomposition has a delay, there is always a background of fouled area, regardless of dung beetle presence. However, even in the absence of dung beetle activity, the decomposition rates are high enough to limit the fouled area to < 0.25% of the total productive area. Another factor is the meat price; in our study it was only 6.2% of that reported by Losey and Vaughan (2006). A third factor is the methodology; we explicitly take into account the temporal dynamics of dung production and decomposition and their effect on the fouled area so we could estimate the average area cleaned by the dung beetles and how it translates into cattle productivity.

For milk, comparisons are difficult. Usually, in temperate zones, milk is produced by specialized cattle breeds raised in confined places or by providing additional feedstuff (Bouwman et al., 2005), while in tropical regions milk is produced by cattle raised on grasslands and pastures and are subject to heat stress (Mawson and White, 1971). The modest contribution is in part due to the low productivity and low milk prices for dual-purpose cattle (Vilaboa et al., 2009). Other differences may be due to cattle races and production systems. In these tropical regions, the preferred breeds are derived from the Zebu × Swiss races (Vilaboa and Díaz, 2009), while in temperate and cold zones European-type breeds are preferred. Further, a recent estimate of reduced pasture fouling by Beynon et al. (2015) yielded a savings of US$ 9.4 per cow, again higher than our estimates. As in the previous economic analysis, differences may be due to different prices, land value, grazing season, management practices, and cattle breeds.

In contrast, the indirect economic impact of dung beetles was estimated as their contribution to nitrogen buried as fertilizer and constant cleaning of the grazing surface, and their values were larger than the direct contribution. For nitrogen, we estimate that dung beetles buried 73.4 kg N ha^{-1} y^{-1}, SD = 27.3, 95% CI (32.2, 136.2), for which the mean economic value was US$ 70.6 ha^{-1}, SD = 28.7, 95% CI (29.4, 139.5). Considering the entire target cattle population at state level, the average total value (US$ × 10E6) was estimated as 78.3, SD = 33.6, 95% CI (30.9, 159.9) (Fig. 6). Furthermore, the benefit of dung beetles in terms of cleaning services was computed at grassland level as an average contribution of US$ 178.1 ha^{-1}, SD = 51.5, 95% CI (89.3, 286.3), which at state level represents a mean value (US$ × 10E6) of 197.5, SD = 62.6, 95% CI (93.5, 335.1), the largest benefit by dung beetles provided in this tropical region (Fig. 6). The continuous input of nitrogen to the soil shows an opportunity to take advantage of this resource if some components of the cattle production systems were modified to increase productivity; for example, by replacing some grass species with more productive ones, or changing the cattle breeds (Ash et al., 2015; Wahinya et al., 2015).

Based on the previous results, in the state of Veracruz the total annual contribution by dung beetles (US$ × 10E6) had a mean = 276.8, SD = 81.1, 95% CI (140.6, 455.8). In terms of the relative contribution of each service, the most important was by

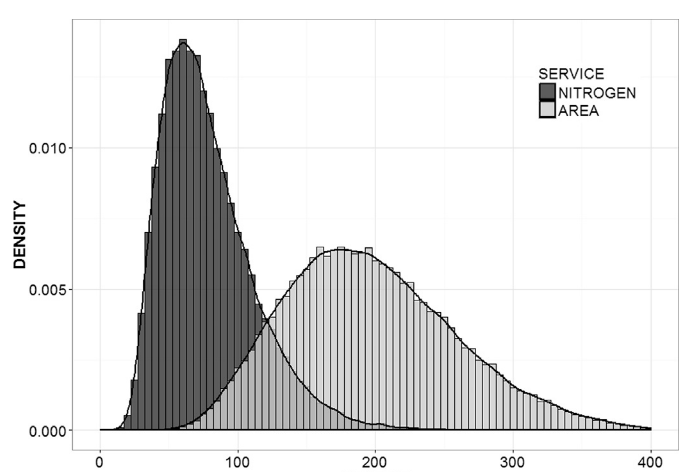

Fig. 6. Sampling distributions of the annual contribution of dung beetles to nitrogen burial (NITROGEN) and clean area (AREA) (US$ × 10E6).

maintaining clean grazing areas, which accounted for a mean of 71.4%, SD = 8.4, 95% CI (53, 85.4). The next important service was by incorporating nitrogen to the soil as fertilizer, with a mean = 28.3%, SD = 8.5, 95% CI (14.4, 46.8). Meat and milk benefits, derived from the direct support of cattle had the smallest values, with a mean = 0.14%, SD = 0.02, 95% CI (0.09, 0.17) and a mean = 0.04%, SD = 0.007, 95% CI (0.03, 0.06), respectively. In addition, on a different scale, the benefits per individual head of cattle (US$ AU^{-1}) were: mean = 274.2, SD = 70.9, 95% CI (149.1, 423.6).

Regarding the value of nitrogen, Losey and Vaughan (2006) found a savings of 17.5 kg per animal; here, our lower point estimate (0.025 percentile) is almost twice. On the other hand, Beynon et al. (2015) reported a savings between US$ 9.8 to US$ 12.2 per cow for nitrogen, phosphorus, and potassium. Therefore, we found higher values for nitrogen burial and its economic benefit. The previously reported estimates most probably derived from the slow decomposition rates yielding less buried nitrogen, and by differences in prices. In the case of nitrogen, it is more expensive in Mexico because much of it is imported (Gaucin and Torres, 2013), therefore it has higher benefit.

Our results differ in many aspects from previous studies by Losey and Vaughan (2006) and Beynon et al. (2015), but also show some similarities. The first similarity is that our research is based on computing the values by contrasting the effects of dung beetles when they are present to when they are not present in a given area, and the second similarity is in using degradation rates. Differences could be considered as extrinsic to the production systems, such as prices, costs, and cattle populations, and intrinsic such as grazing season, climate, management practices, and breeds. Also, another key difference is the modeling approach. All of accounted for differences at cow, grassland and total/state level. Yet, we did not consider other scenarios, such as the analysis of cattle receiving helminthicide treatments, which accounted for nearly 70% of the state cattle population. Thus, additional savings at state level could be expected. We explicitly considered seasonal variation in degradation rates based on the present dung beetle communities (Cruz et al., 2012), and we also considered cattle age classes to standardize the computations on a per animal basis. A key difference is that our model integrates both dung production and degradation rates to obtain a balance in dung occurrence under field conditions, from which we were able to obtain the net effect of dung beetles on milk, meat, nitrogen burial and maintaining clean grasslands. In addition, we were able to compute the variability of these estimates to evaluate conservative and optimistic scenarios for a given condition.

In the case of cleaning service, to our knowledge this is a novel assessment; we assumed that if the dung beetles maintain a clean area, then it is more difficult for flies and parasites to co-occur. We were also able to relate the cleaning service to an alternate practice, which employs machinery, but our estimate is conservative because using human labor is more expensive and so we discarded this approach. Though we did not include gastrointestinal parasites and fly pests, theoretically it is possible their occurrence linked to *Ab* (Fig. 1) because of the delay in dung decomposition. Although there is no clear relationship between dung pats and gastrointestinal parasite or fly populations, cattle producers usually take a risk-averse position and apply parasiticides as a safety procedure, involving costs around US$ 84 per cow per year (Vilaboa and Díaz, 2009; Huerta et al., 2013) but the long-term effect may result in reduced dung degradation rates and reduced dung beetle populations and species diversity (Jacobs and Scholtz, 2015). Also, in Veracruz, the horn fly *Haematobia irritans* (L.) is an important pest, 37% of cattle producers currently spend between US $2.9 to US$ 16.2 per cow per year to control this insect (López-García, 2015). Thus, additional modeling efforts are required to include these and other factors, such as the estimation of effects on greenhouse gas emissions (Slade et al., 2016) which could be studied by including equations to model methane and nitrous oxide emissions (Penttilä et al., 2013).

Although our proposed model considered the dynamics of dung on tropical grasslands and the variability of the factors involved, it still needs to address other elements to increase its scope. For example, the model does not include the spatial variability expected at the state level, where differences in dung beetle abundance and diversity should have an impact on the estimates over large areas (Cabrero-Sañudo et al., 2010). Species composition and abundance are key factors involved in dung degradation, because dung beetle species have different feeding habits and degrade dung at different rates. For example, species of the Scarabaeinae subfamily dominate tropical and temperate zones and 85% are tunnelers, while the Aphodiinae species are usually smaller and feed directly on the dung, being tunnelers more efficient in removing dung than dwellers (Huerta et al., 2013; Nervo et al., 2014). Also, dung beetle communities with more diversity correlated positively with higher dung removal rates (Slade et al., 2011) and beetles with a large body and biomass removed more dung than smaller ones (Nervo et al., 2014; Ortega-Martínez et al., 2016). Also, cattle population has an uneven distribution across the different state municipalities (Vilaboa and Díaz, 2009; Diaz-Rivera et al., 2011). The model only simulates dung dynamics, but it could be connected to a productivity model to take into account grass species, cattle breeds, and management to improve estimates of milk and meat yield (Wahinya et al., 2015). However, by proposing this simulated modeling approach, we expect to open other research avenues to increase our knowledge about the contributions of this insect group to cattle productivity and agroecosystem health.

4. Conclusion

We developed a stochastic simulation model based on the dynamics of dung production and degradation to study the impact of dung beetle activities on dual-purpose cattle productivity in the tropical grasslands of Veracruz, Mexico. The model provided estimates of key biological processes, benefits, and their variability. Most of the cattle are managed with low input technology, reflecting an average density of 0.91 animal units per hectare. Dung pat occurrence was estimated as 44.3 depositions ha^{-1} d^{-1}, and pats removed by dung beetles numbered 88.3 depositions ha^{-1} d^{-1}. The effect of dung removal translated into a clean area of 16.8 m^2 ha^{-1} d^{-1}. On an annual basis, the clean area provided a modest direct savings in milk and meat production, with values of US $ 0.12 and US$ 0.34 ha^{-1}, respectively. Nitrogen buried as fertilizer was estimated as 73.4 kg N ha^{-1} with a value of US$ 70.6 ha^{-1} and the most important contribution was the cleaning service, with a value of US$ 178.1 ha^{-1}. On a per animal basis, the more conservative estimate of savings was US$ 149.1, and the most optimistic was US$ 423.6. At state level, the conservative contribution was US$ 140.6 million and the optimistic estimate was US$ 455.8 million. Additional modeling efforts are required to include spatial variability, species composition and other ecosystem services provided by dung beetles.

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