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West African mixed farming systems as meta-ecosystems: a source-sink modelling approach

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Abstract

Nutrient availability is a major limitation of the production of West African mixed farming systems. The fertility of these systems was traditionally sustained by fallowing, and nutrient transfers by livestock from savanna to croplands. However, demographic growth and socio-economic constraints require the agro-ecological intensification of these systems. To understand how agricultural practices and landscape management affect crop production, we built a meta-ecosystem model of nitrogen stocks and fluxes, and we examined different scenarios of fallow management with or without livestock.

Our results suggest that crop production is highly dependent on the source-sink dynamics of nitrogen. Without livestock, maximum crop production is obtained for an intermediate duration of fallowing, highlighting a trade-off between space devoted to production (cropland) and space devoted to fertility restoration (fallow). In presence of livestock, crop production is maximum for a shorter duration of fallowing; it is markedly higher with than without livestock. **This result highlights the positive roles of livestock and fallows as pumps (vectors) of nitrogen from savanna rangeland to cropland, and from fallow land to cropland, respectively.** However, it also highlights the negative relationship between livestock presence and fallowing, suggesting that the optimal configuration of livestock and fallow management is highly context-dependent.

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Overall, we argue that the meta-ecosystem approach is particularly relevant for the study of agro-ecosystems characterized by high spatial heterogeneity. This work can be seen as a first step toward an alternative approach, integrating tools from theoretical ecology for the study of agro-ecosystems which functioning strongly depends on spatial organisation.

Keywords: African mixed-farming system, meta-ecosystem model, fallow, nitrogen, livestock, crop production

1. Introduction

In dry to sub-humid West-Africa, most farms are traditional mixed systems combining crop and livestock production. For a long time, West-African mixed farming systems (WAMFS) were relatively well adapted to the population needs, in the context of subsistence agriculture (Garrity et al., 2012, Jalloh et al., 2012, Sebastian, 2014). However, WAMFS are currently facing important demographic, social, economic and environmental changes (Jalloh et al., 2013). Over the last century, the increase in agricultural production has been achieved mainly by cropland expansion. This led to a gradual disappearance of fallowing and not cultivated areas, a key component of traditional mixed farming systems. This degradation of the natural vegetation and landscape, particularly pregnant in more semi-arid and arid regions, tends to expand to more humid climate area, the new breadbasket of West-Africa countries. These changes are threatening biomass production and soil fertility, mainly through a decrease of carbon and mineral nutrient stocks in soils (Schlecht et al., 2006, UNEP, 2008). In turn, this decrease compromises the sustainability of the whole farming system, with potentially dramatic social and economic consequences. These perspectives have fostered research on fertility management aimed at defining innovative practices that ensure sustainable farming in sub-Saharan Africa (Rufino et al., 2007).

Increasing exogenous inputs of mineral nutrients and organic matter to soils may seem to be the best response to the decrease of soil fertility; however, applying fertilizers is often prohibitive and risky for local farmers. Moreover, the use of exogenous fertilizers is increasingly recognized as a non-sustainable option, mainly because fertilizer production itself is not sustainable in the long run (Tilman et al., 2002). Many soils of WAMFS are lixisols (IUSS Working Group WRB et al., 2006). These nutrient-poor, highly erodible soils are subject to

24 the formation of slaking crusts and to important losses of nutrients through leaching (Sma-
25 ling et al., 1999). Therefore, crop production in these systems is likely to be particularly
26 sensitive to nutrient loss at the landscape level. The soil capacity to prevent nutrient loss,
27 also referred to as nutrient retention capacity, depends on the efficiency of nutrient recycling,
28 which is driven by soil and ecosystem functioning (Barot et al., 2007, Boudsocq et al., 2009)
29 within the spatial components of the landscape, and on nutrient transfers between these
30 components.

31 Since crop production in WAMFS is frequently limited by nutrient availability, we argue
32 that a better understanding of the cycling and transfers of nutrients across agricultural
33 landscapes may help determine spatial organizations maximizing crop production. The key
34 role of nutrient cycling at both ecosystem (Aerts and Chapin III, 1999) and meta-ecosystem
35 levels (Loreau et al., 2003) for primary production has been highlighted in theoretical ecology.
36 For example, primary production in a given ecosystem may widely depend on processes
37 that maintain fertility in the other ecosystems connected to **it through** source-sink dynamics
38 (Loreau et al., 2013).

39 As agro-ecosystems are mosaics of subsystems forming networks of patches connected
40 by fluxes of nutrients, agro-ecosystems are meta-ecosystems (Loreau et al., 2003). In these
41 landscapes, the productivity of crop fields depends on (1) local nutrient cycling within a
42 subsystem, (2) transfers of nutrients between the connected subsystems, and therefore on (3)
43 nutrient balance within each connected subsystem. Therefore, a better spatial organization
44 of the mosaic of landscape subsystems and a better management of nutrient fluxes between
45 subsystems may help increase crop production and its sustainability.

46 We tackle these issues using a modelling approach focusing on WAMFS of the Guineo-
47 Sudanian biome (Le Hou  rou, 2009) at the beginning of intensification processes, when
48 the surface of savanna is still large enough to provide non-limiting rangeland for livestock.
49 WAMFS are highly spatially structured landscapes with two distinct cultivated subsystems
50 surrounding the dwellings, namely, the “compound ring” (intensive crop fields) and the “bush
51 ring” (extensive crop fields), and two non-cultivated subsystems, namely, fallows in the bush
52 ring, and savanna (Figure 1a). Fluxes of nutrient between these subsystems, and the subse-
53 quent connectivity, are well documented (Diarisso et al., 2015, Manlay et al., 2004b, Pruden-

54 cio, 1993).

55 These fluxes mainly rely on livestock movements, crop harvest and on active spreading
56 by farmers of household wastes close to dwellings. Moreover, these factors all vary across the
57 seasons. Therefore, livestock and land-use management (e.g. the proportion of non-cultivated
58 versus cultivated areas) represent the main driving-forces to optimize nutrient retention and
59 nutrient transfers between subsystems, hence, crop production at the landscape scale.

60 To assess how livestock and land-use management can qualitatively affect the optimization
61 of crop production, we developed and analysed a “minimal” (sensu Mooij et al., 2010) mathe-
62 matical model of nutrient stocks and fluxes in a WAMFS. More specifically, we examined how
63 three “driving forces”, namely, the extent of fallow in space and time, the presence/absence
64 of livestock, and the compound ring:bush ring surface ratio, affect crop production at the
65 landscape level. We used the model to identify the optimal spatial organization for crop
66 production, and the mechanisms by which these three driving-forces, individually or in com-
67 bination, affect crop production.

68 [Figure 1 about here.]

69 **2. Model**

70 In this section, we describe the mathematical model that we built for our study. We focus
71 on the well-documented case study in Guineo-Sudanian West Africa (Le Houérou, 2009): the
72 village of Sare Yero Bana, in the High Casamance region of Senegal (N 12.81917, W 14.89024)
73 (Manlay et al., 2002). All the parameters used in the model, their values, dimensions and
74 their definitions are referenced in Appendix A. The equations of the subsystems models for
75 each season and transition event during the year are summarized in Appendix B.

76 *2.1. Spatio-temporal structure of the model*

77 In the following sections, we first present the spatial structure of the model. Then we
78 detail the two time scales considered in the model: the year (annual cycle), and the multi-year
79 duration of the fallow/crop rotation cycle.

80 2.1.1. Spatial structure

81 As for many agro-ecosystems of West Africa, the landscape at Sare Yero Bana is struc-
82 tured in subsystems that are spatially organized in concentric rings around the dwellings
83 (Manlay et al., 2004b). The compound ring (Figure 1a) is the closest to the dwellings and
84 is permanently cropped with staple crops such as cereals (pearl millet *Pennisetum glaucum*
85 L., maize *Zea mays* L., sorghum *Sorghum bicolor* L. Moench). The compound ring bene-
86 fits from organo-mineral inputs as household wastes and livestock manure. Surrounding the
87 compound ring is the bush ring, which is managed more extensively, and alternates cropping
88 for cash (e.g., groundnut *Arachis hypogea*, a legume; Manlay et al., 2002) and fallow (which
89 consists in a succession of plants dominated by Combretaceae and including nitrogen-fixing
90 species; Manlay et al., 2002).

91 The compound and bush rings are surrounded by permanently uncultivated savanna and
92 used as rangeland for livestock. There is thus an intensification of cropping practices from
93 the savanna to the dwellings.

94 Since we focus on crop production, the nutrient dynamics is explicitly represented in
95 the bush and compound rings only. In the model, the compound and the bush rings are
96 considered as subsystems which areas are denoted by α_c and α_b , respectively. The dwellings
97 and the savanna are simply considered as nutrient sources or sinks. We define sources and
98 sinks accordingly to Loreau et al. (2013), where a source (respectively a sink) subsystem is
99 an exporter (respectively an importer) of nutrient within the whole agro-ecosystem. The
100 savanna is assumed a non-limiting source of nutrient; section 4.4 discusses this assumption.
101 The compound and bush subsystems are connected to each other and to the other spatial
102 entities by different fluxes, that gives the model of the agro-ecosystem the form of a meta-
103 ecosystem model.

104 2.1.2. Annual cycle

105 Agricultural practices change over the seasons. Over one year, a short wet season (4-5
106 months), corresponding to the growing period for plants, alternates with a long dry season
107 (7-8 months). The wet season is characterized by erratic rains amounting annually to circa
108 1100 mm (Ardoin-Bardin, 2004). In our model, a year starts at the beginning of the wet

109 season. In the sequel, T denotes the number of days in a year, τ the number of days in a
110 wet season and n represents the number of years considered since year 0. The wet season of
111 year n starts at day $nT + 1$ with sowing, and ends at day $nT + \tau$ with the harvest, which
112 initiates the transition between the two seasons. The dry season lasts from day $nT + \tau$ to
113 day $(n + 1)T$.

114 *2.1.3. Crop-fallow cycle*

115 The crop-fallow rotation is an agricultural practice that runs at the time scale of several
116 years. It affects the spatial and temporal organizations of the agro-ecosystem and generates a
117 particular set of nutrient fluxes. The “rotation ” is defined as the succession of one cropping
118 period followed by one fallow period. If L denotes the duration (in years) of the rotation
119 and L_c the duration of the cropland period, then $L_f = L - L_c$ is the duration of the fallow
120 period.

121 The bush subsystem includes multiple crop fields and fallow lands. To account for this
122 heterogeneity and to ensure that the cultivated part of the bush ring is constant over time,
123 the bush subsystem is split into L subunits of the same area that will alternatively be in a
124 state of cropland or fallow. At each instant, among the L subunits, L_c and L_f subunits are
125 in states of cropland and fallow, respectively. With this mathematical trick, L (respectively
126 L_c and L_f) represents both the duration (in years) of a rotation (respectively a cropping
127 period and a fallow period) and the total number of subunits (respectively the number of
128 subunits that are in a state of cropland, and the number of subunits that are in a state of
129 fallow). Thus, the proportions of cropland $\frac{L_c}{L}$ and fallow $\frac{L_f}{L}$ are considered constant over a
130 simulation.

131 For instance, a rotation duration of $L = 20$ years and a cropland period duration of
132 $L_c = 15$ years implies a fallow period duration of $L_f = 5$ years. In that case, the bush
133 subsystem is split into 20 subunits with at any time during the rotation, 15 subunits in a
134 state of crop and 5 in a state of fallow. The proportion of subunits in a state of cropland is
135 constant and equal to $\frac{15}{20}$.

136 *2.2. Compound and bush subsystems*

137 The same generic model is used to represent the compound and bush subsystems (Figure
138 1b). This model focuses on the cycle of nitrogen (N), which is usually considered as the
139 main limiting nutrient for crop production in Guineo-Sudanian West Africa (Pieri, 1992,
140 Rufino et al., 2006, Smaling et al., 1999). Though some processes that are specific to N
141 (such as the biological N fixation) are taken into account in the model, adapting the model
142 to phosphorus, which is the other main nutrient limiting primary productivity in these agro-
143 ecosystems (Brouwer and Powell, 1998) would be easy. The subsystem model considered is a
144 N stocks and fluxes model composed of several interconnected N compartments. Fluxes of N
145 between compartments within the subsystem and between the different subsystems depend
146 on the subsystem and on the season (Table 3). The different compartments and fluxes of
147 one subsystem are presented in the following paragraphs. N stocks and fluxes are expressed
148 respectively in kgN per hectare (kgN ha^{-1}), and in kgN per hectare and per day (kgN ha^{-1}
149 day^{-1}) of the subsystem they belong to.

150 *2.2.1. Nitrogen compartments*

151 Each subsystem is composed of three compartments: the plant (P), the soil organic
152 fraction (O) and the soil inorganic fraction (I), to which a fourth compartment, the dead
153 roots of woody plants (R), is added in the case of the bush ring (Figure 1b).

154 The P compartment represents the quantity of nitrogen contained in the plant (both
155 the aboveground and underground parts) per surface unit (kgN ha^{-1}). Each subsystem is
156 assumed to contain one type of plant. In fallow, possible changes in digestibility and palata-
157 bility of plants over time are not considered. For simplicity, we assume that in the compound
158 subsystem and the cropland subunits of the bush subsystem, the plant compartment P con-
159 tains live crop biomass during the wet season, and crop residues (straw, litter, dead-roots)
160 during the dry season. The O and I compartments represent the quantities of nitrogen un-
161 der organic and inorganic forms contained in the first 30 cm of soil per surface unit (kgN
162 ha^{-1}), respectively. The R compartment represents the quantity of nitrogen contained in the
163 belowground part of the woodyplants growing in the bush subsystem during fallow periods.

164 For a subunit j (with $1 \leq j \leq L$) of the bush subsystem, the compartments P , O , I and

165 R are denoted P_j , O_j , I_j and R_j respectively, and are expressed in kgN per hectare of the
 166 subunit j [kgN (ha of bush subunit j)⁻¹]. Within the bush subsystem, the mean biomass of
 167 fallow plants (in kgN per hectare of fallow) is denoted P_{bf} and the mean biomass of crop
 168 plants (in kgN per hectare of bush crop) P_{bc} . See equations (10) and (11) in appendix for
 169 details.

170 Within the compound subsystem, the compartments P , O and I are simply denoted P_c , O_c
 171 and I_c . They are expressed in kgN per hectare of compound ring [kgN (ha of compound)⁻¹].

172 [Table 1 about here.]

173 2.2.2. Intra-subsystem fluxes

174 The model includes five intra-subsystem fluxes (Figure 1b) that connect the different
 175 nitrogen compartments to each other:

- 176 • the growth of the plant compartment P through the uptake of inorganic nitrogen coming
 177 from I (growth function G) and the biological fixation of atmospheric N in the case of
 178 legumes (growth function F) during the wet season
- 179 • the decay of the plant compartment P into soil organic matter O at rate c during the
 180 dry season (this process is considered negligible during the wet season)
- 181 • the transfer of nitrogen located in roots from the plant compartment P (only for woody
 182 plants) to the dead root compartment R (parameter δ), which only occurs in the bush
 183 subsystem during the shift from fallow to cropland after clearing (cf. 2.3.3). We indeed
 184 assume that roots die only when the fallow is cleared at the end of the fallow
- 185 • the decay of the dead-root compartment R which decomposes into soil organic matter
 186 O at rate R , which only occurs in the bush subsystem since R compartment is specific
 187 to it
- 188 • and the mineralization of organic matter O into inorganic nitrogen I at rate m .

189 Intra-subsystem fluxes are all linear and proportional to the amount stored in the com-
 190 partment they originate from, except for plant growth function G (1). G is a modified logistic

191 function with a carrying capacity K and a growth rate u proportional to the stock of inorganic
 192 nitrogen I :

$$G(P, I) = uI \frac{K - P}{K} P \quad (1)$$

193 In the fallow subsystem, the carrying capacity is the plant biomass at equilibrium in ab-
 194 sence of herbivore (May and McLean, 2007). In cultivated subsystems, the carrying capacity
 195 represents the maximum stand biomass at the end of the wet season. In addition to the as-
 196 simation of soil inorganic nitrogen I through the plant growth function G (1), atmospheric
 197 N is assimilated by legumes through symbiotic fixation: groundnut in cropland subunits of
 198 the bush subsystem, and wild species (as *Piliostigma*, *Indigofera spp.*, ...) in fallow subunits.
 199 We assume that the function F (2) describing the atmospheric N fixation is logistic, with a
 200 carrying capacity similar to that of G , and with a biological fixation rate i_p :

$$F(P) = i_p \frac{K - P}{K} P \quad (2)$$

201 To account for the variations of fertility in cultivated subunits of the bush subsystem, the
 202 carrying capacity K is reset every year. In each cultivated subunit j of the bush subsystem,
 203 the carrying capacity K_j (3) is assumed proportional to the value of the compartment I at
 204 the beginning of the wet season:

$$K_j = \min(\omega I_j(nT), K_{\max}), \quad (3)$$

205 ω being a constant parameter and K_{\max} the maximum carrying capacity in absence of limi-
 206 tation by soil inorganic nitrogen. In the fallow subunit j of the bush subsystem $K_j = K_{bf}$.

207 2.2.3. Inputs and outputs of nitrogen from and to the outside

208 In addition to the intra-subsystem fluxes, there are also some inputs and outputs of ni-
 209 trogen entering or exiting the agro-ecosystem. We have represented the inputs of nitrogen
 210 through dry and wet atmospheric depositions of mineral (parameter i_n) and organic (param-
 211 eter i_o) nitrogen.

212 Sowing is considered as an additional punctual input of nitrogen that occurs at the be-
 213 ginning of the wet season. At this instant, the stock in the P compartment of the compound
 214 and bush subsystems is initialized at a value σ (in kgN ha⁻¹), except for the fallow subunits

215 of the bush ring that were already fallow the year before. σ is the quantity of nitrogen
216 contained in seeds sown per hectare. When shifting from cropland to fallow, the nitrogen
217 stock in the seed bank from which fallow vegetation develops is spontaneously present in the
218 environment. Losses of nitrogen from the compartments O and I passively occur through
219 erosion, leaching, volatilization and denitrification. In the model, the parameters e_o and e_n
220 account for the overall loss rates of organic and mineral nitrogen, respectively.

221 *2.3. Inter-subsystems fluxes*

222 The compound and bush subsystems are finally connected to each other through inter-
223 subsystems fluxes. Two types of nitrogen fluxes connect the subsystems, namely, the spread-
224 ing of household wastes from dwellings and the excretion of nitrogen by livestock. Household
225 wastes are spread in the compound subsystem. They mainly originate from crops harvested
226 in both the compound and the bush subsystem, and therefore generate an indirect flux of
227 nitrogen from the bush to the compound subsystem. Livestock generate fluxes of nitrogen
228 between subsystems, and between the savanna and the subsystems, by ingesting nitrogen
229 through grazing during the day, and by excreting nitrogen during day and during night cor-
230 ralling through urine and faeces. Each of these fluxes is detailed in the following paragraphs.

231 *2.3.1. Harvest and recycling fluxes*

232 Crops from the compound subsystem fulfil most staple food needs of villagers, the rest
233 coming from a small part of crops produced by the bush subsystem (Vigan, 2013). The rest
234 of the crops produced by the bush subsystem is exported outside the village. Therefore,
235 there is no exportation of nitrogen through the crop produced in the compound subsystem,
236 whereas most of the nitrogen of the crop produced in the bush subsystem is exported from
237 the agro-ecosystem.

238 The parameter γ represents the share of harvested plant, and the parameter ϵ represents
239 the share of harvested cash crop that is exported from the agro-ecosystem. The quantity of
240 crop $V(n)$ brought to the dwellings after the harvest for a year n is therefore:

$$V(n) = \underbrace{\alpha_c \gamma_c P_c (nT + \tau^-)}_{\text{from compound subsystem}} + \underbrace{\frac{L_c}{L} \alpha_b \gamma_{bc} (1 - \epsilon) P_{bc} (nT + \tau^-)}_{\text{from bush subsystem (cropland subunits)}} \quad (4)$$

241 where $nT + \tau^-$ is the time just before $nT + \tau$, at the end of the wet season, before the
 242 harvest. A share λ_v of $V(n)$ is recycled in the agro-ecosystem and spread during the year in
 243 the compound subsystem as organic amendment. We assume that the spreading is constant
 244 over the year, and that the entire quantity $V(n)$ for year n is consumed within the following
 245 year. Thus, the daily quantity of nitrogen spread in the compound subsystem from day
 246 $nT + \tau + 1$ to day $(n + 1)T + \tau$ is given by $\frac{\lambda_v V(n)}{T}$.

247 2.3.2. Livestock-driven fluxes

248 We assume that livestock grazing follows a Monod function characterized by the half-
 249 saturation constant for feed ingestion κ_κ (in kgN ha⁻¹) and a maximal grazing rate g_{\max}
 250 (in day⁻¹). A herd of κ TLU (TLU stands for Tropical Livestock Unit, corresponding to
 251 an average animal of 250 kg of live weight) that graze on a field containing P kgN ha⁻¹ of
 252 palatable plant will ingest $g_{\max} \frac{P}{\kappa_\kappa + P} \kappa \psi$ kgN per day, where ψ is the quantity of nitrogen (in
 253 kgN) per TLU that we assume constant.

254 The quantity of nitrogen ingested by livestock per day in each subsystem will finally
 255 depend on the season, the subsystem, the area of the subsystem, the available plant biomass,
 256 the palatability coefficient of the plants, the time spent in the subsystem, the half-saturation
 257 Monod constant κ_κ for feed ingestion and the maximal grazing rate g_{\max} .

258 During the wet season the livestock is kept away from crops, graze in fallows and in
 259 the savanna and are corralled at night in fallows. The quantity of nitrogen ingested by the
 260 livestock per day in the fallow is therefore given by $\zeta_{wet} g_{\max} \frac{b_{bf} P_{bf}}{\kappa_\kappa + b_{bf} P_{bf}} \kappa \psi$ (in kgN day⁻¹) where
 261 ζ_{wet} is the percentage of time spend by the livestock in fallows, the other part of the day
 262 being spent in savanna or corresponding to the night, and b_{bf} is the palatability coefficient
 263 of the fallow plants. In this quantity, the part coming from the fallow subunit j of the bush
 264 ring is given by:

$$\phi_{wet}^j = \zeta_{wet} g_{\max} \frac{b_{bf} \frac{1}{L_f} P_j}{\kappa_\kappa + b_{bf} P_{bf}} \kappa \psi \quad (\text{kgN day}^{-1}) \quad (5)$$

265 During the dry season the livestock grazes all over the landscape, and are corralled in
 266 the compound subsystem at night. The concentration of nitrogen contained in the palatable
 267 plants in the bush and compound rings, that we denote P_{tot} , is given by:

$$P_{tot} = \frac{\frac{L_f}{L}\alpha_b b_{bf} P_{bf} + \frac{L_c}{L}\alpha_b b_{bc} P_{bc} + \alpha_c b_c P_c}{\alpha_b + \alpha_c} \text{ in kgN per ha of bush+compound} \quad (6)$$

268 where b_{bc} and b_{bf} are the palatability coefficients of the plants in the cropland part of the
 269 bush ring and in the compound ring, respectively. The quantity of nitrogen ingested by the
 270 livestock per day in the bush and compound rings is therefore given by $\zeta_{dry} g_{\max} \frac{P_{tot}}{\kappa_{\kappa} + P_{tot}} \kappa \psi$
 271 (in kgN day⁻¹) where ζ_{dry} is the percentage of time spend by the livestock on the bush and
 272 compound rings, the other part being spend in savanna or corresponding to the night. In
 273 this quantity, the part coming from the compound subsystem is:

$$\phi_{dry}^c = \zeta_{dry} g_{\max} \frac{\frac{\alpha_c b_c P_c}{\alpha_b + \alpha_c}}{\kappa_{\kappa} + P_{tot}} \kappa \psi \quad \text{kgN day}^{-1} \quad (7)$$

274 and the part coming from the subunit j (crop or fallow) of the bush subsystem is

$$\phi_{dry}^j = \zeta_{dry} g_{\max} \frac{\frac{1}{L} \frac{\alpha_b b_j P_j}{\alpha_b + \alpha_c}}{\kappa_{\kappa} + P_{tot}} \kappa \psi \quad \text{kgN day}^{-1} \quad (8)$$

275 with $b_j = b_{bc}$ for a cropland subunit j of the bush subsystem and $b_j = b_{bf}$ for a fallow subunit
 276 j of the bush subsystem. We assume that feed requirements of livestock is always met and
 277 remain constant over time. Hence, a fixed *per-capita* quantity ρ of nitrogen has to be ingested
 278 daily (in kgN TLU⁻¹ day⁻¹), which amounts to a total quantity $\kappa \rho$ (in kgN day⁻¹).

279 The savanna is a feed reservoir exploited only when cultivated areas cannot fulfil livestock
 280 requirements. In this case, the complement of feed provided by the savanna per day is given
 281 by $\kappa \rho - \sum_{j=1}^L (1 - \theta_j) \phi_{wet}^j$ (in kgN day⁻¹) during the wet season and by $\kappa \rho - \phi_{dry}^c - \sum_{j=1}^L \phi_{dry}^j$
 282 (in kgN day⁻¹) during the dry season, where $\theta_j = 1$ when the subunit j is under cropping and
 283 $\theta_j = 0$ when the subunit j is under fallowing. The presence of livestock in the agro-ecosystem
 284 induces additional losses due to metabolic constraints: a percentage λ_{κ} of the feed ingested is
 285 excreted, the rest being used for growth and reproduction. We assume that livestock biomass
 286 is kept constant and that N allocated to growth and reproduction is exported outside the
 287 agro-ecosystem (for instance, through the sale of meat). A proportion ν of the excreted
 288 nitrogen returns to the soil as urine (compartment I); the remaining part $(1 - \nu)$ returns

289 to the soil as organic nitrogen (compartment O) through the deposition of faeces. Overall,
 290 livestock transfers nitrogen from savanna to the bush subsystem during the wet season, and
 291 to the compound subsystem during the dry season. Animals feed exclusively during the
 292 day but excretes almost equally during day and night (Manlay et al., 2004c). Thus, night
 293 corralling generates a net transfer from feeding grounds to the corral. The parameter h
 294 represents the proportion of excretion that occurs during the day, when livestock is grazing,
 295 and $(1 - h)$ is the proportion of excretion that occurs during the night, when livestock is
 296 corralled. Consequently, the quantity of nitrogen excreted during one day in a subsystem (or
 297 subunit j of a subsystem) only depends on the quantity ϕ of nitrogen ingested during this
 298 day in this subsystem (or subunit j of a subsystem): it equals $h\lambda_\kappa\phi$ (in kgN day^{-1}). During
 299 the night, the quantity of nitrogen excreted in the corral (fallow during the wet season and
 300 compound during the dry season) is constant and equals $(1 - h)\lambda_\kappa\kappa\rho$ (in kgN day^{-1}) (see
 301 Figure 2 for a schematic representation of livestock-induced nitrogen fluxes).

302 [Figure 2 about here.]

303 2.3.3. Fallow-Crop shifts

304 Fallow-cropland shifts occur at the beginning of the wet season, at time nT . These shifts
 305 do not lead to spatial transfers of nutrients, but they change the distribution of nitrogen
 306 among the compartments of the bush subsystem. When shifting from fallow to cropland, the
 307 compartment R of the concerned bush subunit is updated at the beginning of the wet season
 308 to account for the transfer of the roots of senescent fallow biomass to soil organic matter.
 309 Plant stems are cleared and exported outside the agro-ecosystem before the sowing and the
 310 woody part of the roots (percentage δ) of fallow biomass is transferred to the dead roots
 311 compartment R :

$$R_j(nT) = R_j(nT^-) + \delta P_j(nT^-) \quad (9)$$

312 where nT^- is the time just before nT , at the end of the dry season, before the sowing and the
 313 fallow clearing. We assume that R decays exponentially (Manlay et al., 2004c) at rate r and
 314 fuels the soil organic matter compartment O during the years following the shift. According
 315 to Manlay et al. (2004c), more than 95% of dead woody roots are degraded after two years.

316 2.4. Validation of the model

317 The comparison to Sare Yero Bana data is described in appendices, section 6.4. The effect
318 of each parameter of the model on the bush, the compound and the total crop productions
319 was examined through a sensitivity analysis, described in appendices, section 6.5.

320 3. Simulations

321 Crop production depends on available nitrogen. According to the meta-ecosystem theory
322 (Gravel et al., 2010, Loreau et al., 2003), crop production should depend on net inputs of
323 nitrogen into the agro-ecosystem, and on how these inputs are transferred to the subsystems
324 that produce crop. Thus, to identify strategies optimizing crop production, we first need to
325 understand what governs the intensity of the nitrogen inputs into the agro-ecosystem, and
326 then, how these fluxes to cropland subunits and to the compound subsystem are implemented.

327 3.1. The “Fallow Pump” and the “Livestock Pump” as the two main sources of nitrogen.

328 [Figure 3 about here.]

329 Two “ecological pumps”, resulting from source-sink dynamics within the agro-ecosystem
330 should have a major influence on the input of nitrogen to the agro-ecosystem, namely the
331 “Fallow Pump” and the “Livestock Pump” (Figure 3). These terminologies are used by
332 reference to the “whale pump” that brings nutrients from deep to shallower waters in the
333 oceans (Roman and McCarthy, 2010).

334 Fallow land is a source of nitrogen for the bush subsystem because it hosts N_2 -fixing
335 legumes. In addition, fallow efficiently retains soil inorganic nitrogen because leaching is
336 lower than in other subsystems, due to a higher soil cover by plant biomass (Pieri, 1992,
337 Serpantié and Ouattara, 2001). Therefore, fallow subunits accumulate nitrogen, which is
338 then transferred to cropland subunits when fallow subunits are cleared and cultivated. This
339 net input of nitrogen to the agro-ecosystem is referred to as the “Fallow Pump”. On the
340 other hand, livestock transfers nitrogen from grazed savanna, to the bush and compound
341 subsystems, where it is corralled overnight. This overall input of nitrogen to the agro-
342 ecosystem is referred to as the “Livestock Pump”.

343 Fallow and livestock management drives how these two pumps influence the overall input
344 conservation of nitrogen in the agro-ecosystem (Figure 3). In addition, within the agro-
345 ecosystem, livestock management influences how nitrogen is transferred to subsystems pro-
346 ducing crop. Indeed, through grazing and night corralling, animals generate source-sink
347 dynamics between fallow subunits and crop fields subunits within the bush subsystem, and
348 between the bush subsystem and the compound subsystem. These source-sink dynamics vary
349 across seasons.

350 We first studied the system in absence of livestock to understand how to optimize crop
351 production with the Fallow Pump alone. Then, we studied the system in presence of livestock,
352 to understand the effect of the Livestock Pump, the effect of the source-sink dynamics due
353 to livestock, and the interaction between the Fallow and the Livestock Pumps.

354 *3.2. Test of the effect of the pumps*

355 We performed two distinct studies. For all the simulations, we assumed that the total
356 area of the agro-ecosystem was constant and equal to 200 ha, which is roughly the size of the
357 agro-ecosystem of Sare Yero Bana. This surface does not include the surrounding savanna,
358 which is assumed to be infinite. We performed simulations with and without ($\kappa = 0$ TLU)
359 livestock. Simulations with livestock were run with $\kappa = 410$ TLU, which is consistent with
360 the herbivory pressure observed in Sare Yero Bana (Vigan, 2013).

361 The first study we performed focuses on the impact of the fallow extent on the biomass of
362 crop harvested at the end of the wet season in the bush and the compound subsystems. More
363 precisely, we tried to assess the consequences of (1) an increase in the duration of rotation
364 ($L = 10, 20, 50$ and 100 years), and of (2) an increase in the cropland ratio ($0 \leq \frac{L_c}{L} \leq L$).
365 For this first study, we assumed a constant ratio $\alpha_c : \alpha_b$ of 1:3, 50 ha of compound and 150
366 ha of bush, as observed recently in Sare Yero Bana by Vigan (2013).

367 In a second study, we examined how the fraction of the agro-ecosystem occupied by the
368 compound subsystem $\frac{\alpha_c}{(\alpha_c + \alpha_b)}$, hereafter named the “compound ratio”, influences the biomass
369 of crop harvested at the end of the wet season in the bush and the compound subsystems,
370 fallow extent being fixed. There is no variation in spatial organization and practices within
371 one simulation.

372 Simulations were performed with R (R Core Team, 2016) by using the RungeKutta
373 method of the R package “deSolve” (Soetaert et al., 2010) that enables to numerically inte-
374 grate systems of ordinary differential equations. Each simulation (one simulation per set of
375 parameters tested) was performed over 300 years, which was enough to reach the periodic
376 equilibrium of the system. The R package containing all the necessary functions to simulate
377 the model is available on github (https://github.com/AnneBisson/EwocR_2.git).

378 4. Results and Discussion

379 4.1. Managing the Fallow Pump to maximize crop production: the effect of cropland ratio 380 and rotation duration

381 [Figure 4 about here.]

382 The Figure 4a depicts the impact of the cropland ratio $\frac{L_c}{L}$ and the rotation duration L
383 (the colour of the line varies from light to dark as the rotation duration L increases) on
384 crop production in the bush subsystem (i.e. the sum of crop production in all the cropland
385 subunits of the bush subsystem), in absence of livestock. Both affect the Fallow Pump and
386 its effect on crop production in the bush subsystem, with consequences for crop production
387 in the compound subsystem.

388 Regardless of the rotation duration, when the cropland ratio increases from 0 to 1, crop
389 production in the bush subsystem increases from 0 to a maximum π_{\max} , then decreases and
390 finally slightly re-increases when the cropland ratio reaches 1.

391 The humpback shape of the curves is consistent with previous results obtained with a
392 simpler mathematical model by Robertson (1994) and Mobbs and Cannell (1995) in their
393 study of a generic *Sorghum bicolor* - *Acacia Senegal* agro-system. In our model, as in the
394 model of the latter, this humpback curve results from a trade-off between the increase in crop
395 production due to the increase in the area cultivated, and the decrease of the restoration of
396 soil fertility by fallow. Indeed, as the cropland ratio increases, the cultivated area increases,
397 entailing an increase in crop production. However, the decrease of fallow leads to a loss of
398 fertility that translates into lower yields, which finally leads to a decrease of crop production
399 at the subsystem level.

400 In our model, the cropland ratio that leads to π_{\max} varies with the rotation duration, with
401 the overall maximal production (3233 kgN yr⁻¹) reached for a rotation duration of 50 years
402 and a cropland ratio of 0.67. The observation of a crop production without fallow higher than
403 with few years of fallow suggests that short fallow time do not restore soil fertility enough in
404 terms of nitrogen stock to compensate for the cropping area reduction it demands. This trend
405 is consistent with other studies (Aweto, 1981, Brand and Pfund, 1998, Roder et al., 1997);
406 it is even an assumption in some fallow models Aweto (2012). In the first years of fallow,
407 soil fertility decline is usually thought to result from an inadequate vegetation cover during
408 the early succession of natural vegetation recovery, but the model suggests an alternative
409 explanation. In simulations, the inflection results from slow restoration of the soil organic
410 nitrogen stock during the very first years of fallowing and to a much lower growth rate of
411 fallow than cropped plants (0.005 and 0.01 ha kgN⁻¹ y⁻¹, respectively). As a result, the net
412 balance of nitrogen after a short fallow time is negative: the impact of the Fallow Pump is
413 thus negative. According to our simulations, the number of years of fallow (4 years) beyond
414 which fallow has a positive impact on productivity is independent of the rotation duration
415 (Figures 4a). On the other hand, if the fallow period is long enough, dead-roots (R) and soil
416 organic matter (O) accumulations reach a maximum. Once this maximum is reached, from
417 a biogeochemical viewpoint it is no more profitable to maintain fallowing.

418 The comparison between curves of the Figure 4a shows that the cropland ratio leading to
419 the maximal crop production π_{\max} increases with the rotation duration. Among the differ-
420 ent rotation duration scenarios, the highest crop production is reached for an intermediate
421 rotation duration π_{\max}^{50} . This is because crop production is driven by the combination of
422 two mechanisms. First, for short rotation durations, fallow duration is too short to restore
423 soil fertility. Second, for long rotation durations, large accretion in soil organic and mineral
424 nitrogen during prolonged fallowing does not balance declining yields at the end of longer
425 cropping periods. For a given cropland ratio indeed, a longer rotation duration translates
426 into longer cropping duration and not just longer fallow duration.

427 Figures 4b-c show that the increase in crop production in the compound subsystem and in
428 the agro-ecosystem as the whole is correlated to the increase in crop production in the bush
429 subsystem. Indeed, the redistribution of fertilizing household wastes to the compound sub-

430 system generates a source-sink dynamics from the bush to the compound subsystem, because
431 part of these wastes comes from crop production in the bush subsystem. As a consequence
432 of this simple source-sink dynamics, the trends observed in the compound subsystem (Figure
433 4b) and in the whole agro-ecosystem (Figure 4c) are similar to the trends observed in the
434 bush subsystem (Figure 4a).

435 The Figure 5 represents the balance of N fluxes (in $\text{kgN ha}^{-1} \text{y}^{-1}$) of the compound
436 subsystem and the bush subsystem (crops and fallow) over the last year of a 300 years
437 simulation without (0 TLU) and with (410 TLU) livestock for three cases of the simulations
438 represented in the Figure 4, corresponding to a cropland ratio $\frac{L_c}{L} = 0.25, 0.5$ and $0.75,$
439 respectively. Without livestock, biological fixation represents the main source of nitrogen for
440 the agro-ecosystem. Looking at the three detailed cases, N fixation decreases in cropland
441 subunits as the cropland ratio increases. On the other hand N fixation in fallows is maximal
442 for an intermediate value of cropland ratio ($\frac{L_c}{L} = 0.5$).

443 4.2. Managing the Livestock Pump to maximize crop production

444 Figures 4d-f depict the impact of increasing the cropland ratio $\frac{L_c}{L}$ and the rotation dura-
445 tion L on crop production in the bush subsystem, in the compound subsystem, and in the
446 whole agro-ecosystem, respectively, in the presence of livestock.

447 The activation of the Livestock Pump strongly modifies the functioning of the agro-
448 ecosystem. Strikingly, crop production of the whole agro-ecosystem increases sharply (Fig-
449 ures 4f), mainly driven by the increase in crop production in the compound subsystem (Fig-
450 ures 4e). This gain of production highlights the Livestock Pump as the main importer of
451 nitrogen to the agro-ecosystem, through a source-sink dynamics from the savanna to the
452 compound ring. In addition, within the agro-ecosystem, livestock generates source-sink dy-
453 namics between the subunits of the bush subsystem, and between the bush and the compound
454 subsystems. These dynamics strongly affect the way the gain in nitrogen from the Livestock
455 Pump is transferred to crop production in the compound subsystem.

456 During the wet season, livestock mainly grazes in the savanna and is corralled at night
457 in the fallow subunits where it does not graze and where it excretes some of the nitrogen
458 ingested during the day. Hence, the Livestock Pump fuels the fallow subunits only. The
459 gain of nitrogen adds up to the Fallow Pump and is transferred to the cropland subunits and

460 crop production when fallow subunits are cleared and cultivated. During the dry season, the
461 situation drastically changes. Livestock grazes both in the savanna and in the agro-ecosystem
462 and is corralled at night in the compound subsystem, where it excretes nitrogen. Hence, the
463 Livestock Pump fuels the compound subsystem. The variation of range in N balance (Figure
464 5) in the compound ring shows how the inputs of N by livestock leads to significant losses of
465 N.

466 The Livestock Pump has a positive effect on crop production in the compound subsystem
467 (Figure 4e). However, it may or may not have a positive effect on crop production in the
468 bush subsystem, depending on the management of the Fallow Pump (Figure 4d). In the
469 case of short rotation durations (≤ 20 years, see Appendix C, section 6.4) the Livestock
470 Pump has a net positive effect on the stock of nitrogen in the fallow subunits, regardless of
471 the cropland ratio $\frac{L_c}{L}$. Through fallow to crop conversion, this fertility is transferred to the
472 cropland subunits and increases crop production in the bush subsystem.

473 On the other hand, for longer rotation durations, the Livestock Pump has a positive effect
474 on crop production of bush subsystem only for high cropland ratios (e.g., $\frac{L_c}{L} > 0.8$ for $L = 100$
475 years, as depicted in Figure 4). The reason is that for lower cropland ratios, the quantity
476 of feed provided by fallow covers a large part of the requirement of livestock during the dry
477 season. Therefore, livestock mostly grazes in the bush subsystem and transfers the ingested
478 nitrogen to the compound subsystem during night corraling. This mechanism has two main
479 effects, (1) it weakens the Livestock Pump since there is less transfer from savanna to the
480 agro-ecosystem during the dry season, and (2) it increases the source-sink dynamics from
481 the bush to the compound subsystem. As a result, crop production in the bush subsystem
482 is lower in the presence than in the absence of livestock.

483 With livestock, the maximum crop production is always reached for $L_c = L - 1$, which
484 corresponds to the shortest possible fallow ratio. Fallows must at least exist in its minimum
485 form to allow livestock corraling and the functioning of the livestock pump. As a result, the
486 negative effect of too short fallow without livestock is no longer observed because in addition
487 to the weak effect of restoring fertility, livestock corraling in fallows during the wet season
488 concentrates nutrient in fallows. Finally, fallows tend to annihilate the Livestock Pump since
489 the agro-ecosystem is less dependent on nutrients from the savanna.

490 [Figure 5 about here.]

491 *4.3. Managing spatial organization to maximize crop production*

492 [Figure 6 about here.]

493 The connectivity introduced by livestock between the bush and the compound subsys-
494 tems lead to an interdependency of these two compartments of the landscape. Given this
495 interdependency, crop production of the whole agro-ecosystem is expected to depend on the
496 compound:bush subsystem areas, referred to hereafter as the “compound ratio”. The influ-
497 ence of the compound ratio on crop yield (in kgN ha⁻¹) and total crop production (in kgN)
498 in each subsystem and at the whole agro-ecosystem level is examined (Figure 6), in presence
499 of livestock. We assumed a rotation duration of 20 years, and a cropland ratio of 0.25, that
500 is 5 years of cropland followed by 15 years of fallow. This scenario is similar to the situation
501 in Sare Yero Bana (Manlay et al., 2004b,a).

502 For this scenario, both the yield and the total production follow a humpback curve when
503 the compound ratio increases. The optimal total production is obtained for a compound ratio
504 of 0.3, whereas the optimal yield is obtained for a compound ratio of 0.25. This mismatch
505 results from the fact that sub-optimality of the yield when the ratio increases is overbalanced
506 by the increase in total cropland area, which increases the production at the agro-ecosystem
507 level. In fact, increasing the compound ratio has both a positive and negative effect on the
508 total production. The positive effect arises from the increase in the area devoted to crop
509 production. The negative impact results from the dilution of the source-sink effect: when
510 the compound ratio increases, the source (the bush subsystem) decreases and the sink (the
511 cropland subsystem) increases in size. Therefore, the flux of nitrogen imported by livestock
512 from bush to cropland decreases and is diluted over an increasing area of cropland.

513 *4.4. The hidden gain from savanna*

514 In the model, a fraction of the nitrogen ingested by livestock exits the agro-ecosystem
515 through meat exportation. Over a year, livestock intakes 14.9 tN (the quantity of nitrogen
516 ingested by 410 TLU, that is $\rho\kappa T$) and excretes 11.9 tN through urine and faeces ($\lambda_{\kappa}\rho\kappa T$).
517 A fraction of the consumed nitrogen comes from the fallow subunits of the bush subsys-
518 tem where livestock grazes during the dry season, the rest coming from the savanna. The

519 proportion of time spent feeding in the fallow versus the savanna determines the respective
520 contribution of these two sources. Our model assumes that livestock always fulfils its nitro-
521 gen requirement. It first consumes what is available in the agro-ecosystem, then satisfies its
522 nitrogen requirements with nitrogen from the savanna. Thus, if the cropland ratio increases
523 within the bush subsystem and/or if the compound ratio increases, the area of land occupied
524 by fallow decreases, entailing a higher contribution of savanna as a source of nitrogen. As-
525 suming a herd of 410 TLU, for a cropland ratio of 0.25 and a rotation duration of 20 years,
526 the savanna provides 50 % of the nitrogen ingested by livestock (7045 kgN that represent
527 about 1300 ha of savanna considering numbers given by Powell et al. (1996) for Sahelian
528 areas or by Abbadie et al. (2006) for Lamto savanna). With the same rotation duration and
529 a cropland ratio of 0.75, the savanna represents more than 70 % of the nitrogen ingested by
530 livestock, becoming the main source of nitrogen for the agro-ecosystem. This dependency on
531 savanna raises the question of the sustainability of crop production in the agro-ecosystems
532 of West Africa, where agriculture is encroaching on savanna. In this context, savanna area
533 may become a limiting resource, constraining the size of livestock herds and thus, the net
534 input of nitrogen to the agro-ecosystem (Vayssières et al., 2015). In addition to this decrease
535 of the Livestock Pump, the agriculture evolution in a demographic growth context generally
536 comes together with a shortening of the rotation duration and an increase in the cropland
537 ratio, which reduces the N source provided by legumes in fallows, and thus, decreases the
538 Fallow Pump. The reduction of N source could be offset by an increase of legume-cereal
539 crop rotation or intercropping as it is the case in the groundnut basin. There is an other
540 limit according to Liebig's law: the availability of P, which can only be increased by the
541 application of mineral fertilizers, or by the possible (but not yet certain) increase of P by the
542 deep root systems of the trees (need for agroforestry). Some farmers facing such a reduction
543 of accessible savanna manage to maintain large herds of livestock by feeding animals with
544 exogenous supplementation (Audouin et al., 2015). Doing so, they maintain the Livestock
545 Pump, but they replace economical and ecological costless nitrogen provided by savanna by
546 economical and ecological costly nitrogen.

547 To take into account this cost, our modelling work calls for an explicit representation of
548 the savanna as a finite source of nitrogen, and an explicit representation of the dynamics

549 of nitrogen in livestock. Such improvement would allow (1) assessing whether the nutrient
550 provisioning by savanna is sustainable or not, (2) measuring the livestock production and
551 its possible limitations due to nutrient availability, and (3) exploring the potential of other
552 sources of nitrogen such as mineral fertilizers to improve the agroecosystem production.
553 Unlike for traditional agro-ecosystems where savanna is not limiting, we hypothesize that in
554 agro-ecosystems with increasingly limited land in the future (Jayne et al., 2014), new tensions
555 and new trade-offs occur between crop production in the bush versus compound subsystems,
556 and between meat and crop productions. Such situations are likely to occur more often as
557 local human population densities increase, with a subsequent increasing need for croplands.

558 **5. Conclusion**

559 Crop production in WAMFS depends on complex dynamics of nitrogen through the dif-
560 ferent compartments of the agricultural landscape. Despite this complexity, our model, with
561 its “meta-ecosystem” approach, shows that the optimization of crop production relies mainly
562 on a good management of the Fallow Pump and the Livestock Pump that represent the main
563 inputs of nitrogen into the agro-ecosystem. Management must take into account the inter-
564 action between these two ecological pumps to optimize the global input of nitrogen, as well
565 as the role of the livestock as a driving-force to optimize the transfer of this nitrogen flux to
566 the agro-ecosystem’s subsystems that produce crop.

567 More precisely, our results suggest that the Livestock Pump represents a higher input
568 of nitrogen to the agro-ecosystem than the Fallow Pump, and that the Fallow Pump tends
569 to interact negatively with the Livestock Pump. Thus, crop production is optimal when
570 agricultural practices and spatial organizations are such that the agro-ecosystem contains
571 livestock and has a relatively low area devoted to fallow.

572 In addition, our results stress the fact that livestock reinforces the source-sink dynamics
573 between the bush and compound subsystems, that is, between the extensive and intensive
574 part of the agro-ecosystem. This source-sink dynamics is required to transfer the benefit of
575 the Fallow Pump to the productive compound subsystem.

576 A corollary to these results is that crop production by WAMFS is highly dependent on the
577 Livestock Pump and therefore on the savanna as an external source of nitrogen. The optimal

578 practices suggested by our model hold as long as savanna extension is enough not to be a
579 limiting source of nitrogen to livestock. This assumption was likely relevant in traditional
580 WAMFSs, but it should be reconsidered in the context of agriculture extensification where
581 cropland is encroaching on savanna. In this new context, our model could be regarded as a
582 “null model”. This null model could serve as a corner stone to help understand how fertility
583 transfers will evolve according to new management strategies and spatial organization, and
584 to help propose new management practices that will ease the transition towards a more
585 sustainable agriculture.

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592 6. Appendix

593 6.1. Table of variables

Table 1: Variables used in the model. E.v. is for Estimated value

Variable	Eq.	Unit	Description
P		kgN ha ⁻¹	Quantity of N contained in the plant biomass per hectare of a generic subsystem
O		kgN ha ⁻¹	Quantity of N contained in the soil organic fraction per hectare of a generic subsystem
I		kgN ha ⁻¹	Quantity of N contained in the soil inorganic fraction per hectare of a generic subsystem
R		kgN ha ⁻¹	Quantity of N contained in the dead roots of woody plants per hectare of a generic subsystem
X_c		kgN (ha of c) ⁻¹	Quantity of N contained in the stock X , with $X \in P, O, I$, per hectare of compound ring
X_j		kgN (ha of b unit j) ⁻¹	Quantity of N contained in the stock X , with $X \in P, O, I, R$, per hectare of subunit j of the bush ring
⁵⁹⁴ P_{bf}	10	kgN (ha of bf) ⁻¹	Quantity of N contained in the plant biomass per hectare of bush fallow
P_{bc}	(11)	kgN (ha of bc) ⁻¹	Quantity of N contained in the plant biomass per hectare of bush crop
P_{tot}	(6)	kgN (ha of b and c) ⁻¹	Quantity of N contained in the palatable plants per hectare of bush+compound ring
θ_j		-	Current state of the subunit j of the bush ring: $\theta_j(t) = 1$ means that the subunit j is under cropping at time t , $\theta_j(t) = 0$ means that the subunit j is under fallowing at time t .
K_j	(3)	kgN (ha of b unit j) ⁻¹	Carrying capacity of the subunit j of the bush ring
G	(1)	kgN ha ⁻¹ day ⁻¹	Growth function of the plant compartment P through the uptake of inorganic N

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Variable	Eq.	Unit	Description
F	(2)	kgN ha ⁻¹ day ⁻¹	Growth function of the plant compartment P through the atmospheric N biological fixation
ϕ		kgN day ⁻¹	Quantity of N ingested by the livestock per day in a generic subsystem
ϕ_{wet}^j	(5)	kgN day ⁻¹	Quantity of N ingested by the livestock per day in a subunit j of the bush ring during the wet season
595			
ϕ_{dry}^j	(8)	kgN day ⁻¹	Quantity of N ingested by the livestock per day in a subunit j of the bush ring during the dry season
ϕ_{dry}^c	(7)	kgN day ⁻¹	Quantity of N ingested by the livestock per day in a the compound ring during the dry season
$V(n)$	(4)	kgN	Quantity of crop N brought back to the dwellings after the harvest of a year n

596 Within the bush subsystem, the mean biomass of fallow plants (in kgN per hectare of
597 fallow) is expressed by

$$P_{bf} = \frac{1}{L_f} \sum_{j=1}^L P_j (1 - \theta_j) \quad [\text{kgN (ha of fallow)}^{-1}] \quad (10)$$

598 and the mean biomass of crop plants (in kgN per hectare of bush crop) is

$$P_{bc} = \frac{1}{L_c} \sum_{j=1}^L P_j \theta_j \quad [\text{kgN (ha of bush crop)}^{-1}] \quad (11)$$

599 6.2. Table of parameters

Table 2: Parameters used in the model. E.v. is for Estimated value. AS is for Sensitivity Analysis

Param.	Value	Range (AS)	Dimensions	Description and source
u_c	5 10 ⁻³	0.0035 - 0.0065	ha kgN ⁻¹ day ⁻¹	Rate of mineral N uptake by Plant in compound subsystem – E.v.
K_c	80	56 - 104	kgN ha ⁻¹	Carrying capacity (cereals) – Manlay et al. (2002)
c_c	0.01	0.007 - 0.013	day ⁻¹	Decomposition rate of crop residues – E.v.
m_c	1 10 ⁻⁴	7 10 ⁻⁵ - 0.00013	day ⁻¹	Mineralization rate by microorganisms – E.v.
e_{oc}	2 10 ⁻⁴	0.00014 - 0.00026	day ⁻¹	Organic N loss rate – Pieri (1992)
e_{nc}	0.003	0.0056 - 0.0104	day ⁻¹	Mineral N loss rate – Pieri (1992)
u_{bc}	0.01	0.0035 - 0.0065	ha kgN ⁻¹ day ⁻¹	Rate of mineral N uptake by plants in cropland subunits of bush subsystem – E.v.
K_{\max}^{600}	90	63 - 117	kgN ha ⁻¹	Maximum Groundnut carrying capacity – Manlay et al. (2002)
ω	2.5	1 - 5	–	constant parameter in the expression of K_{\max} – E.v.
i_{pbc}	2 10 ⁻²	0.014 - 0.026	day ⁻¹	Biological N fixation by groundnut–Ndiaye (1986)
c_{bc}	1 10 ⁻²	0.007 - 0.013	day ⁻¹	Decomposition rate of crop residues – E.v.
m_{bc}	1 10 ⁻⁴	7 10 ⁻⁵ - 1.3 10 ⁻⁴	day ⁻¹	Mineralization rate by microorganisms – E.v.
e_{obc}	2 10 ⁻⁴	0.00014 - 0.00026	day ⁻¹	Organic N loss rate –Pieri (1992)
e_{nbc}	5 10 ⁻³	0.0035 - 0.0065	day ⁻¹	Mineral N loss rate – Pieri (1992)
u_{bf}	5 10 ⁻⁵	0.0035 - 0.0065	ha kgN ⁻¹ day ⁻¹	Rate of mineral N uptake by plants in fallow subunits of bush subsystem – E.v.
K_{bf}	350	245 - 455	kgN ha ⁻¹	Carrying capacity (fallow) – Manlay et al. (2002)

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Param.	Value	Range (AS)	Dimensions	Description and source
i_{pbf}	$6 \cdot 10^{-4}$	0.0042 - 0.0078	day ⁻¹	Biological N fixation by plants – Buerkert and Hiernaux (1998)
c_{bf}	$8 \cdot 10^{-4}$	0.00056 - 0.00104	day ⁻¹	Plant mortality during dry season – Buerkert and Hiernaux (1998)
m_{bf}	$1 \cdot 10^{-4}$	10^{-5} - 0.00013	day ⁻¹	Mineralization rate by microorganisms – E.v.
e_{obf}	$2 \cdot 10^{-4}$	0.00014 - 0.00026	day ⁻¹	Organic N loss rate – Buerkert and Hiernaux (1998)
e_{nbf}	$1 \cdot 10^{-3}$	0.0007 - 0.0013	day ⁻¹	Mineral N loss rate – Buerkert and Hiernaux (1998)
λ_{κ}	80	60 - 95	%	Percent of N intake excreted by livestock – Manlay et al. (2004b)
κ	410	0 - 1000	TLU	Size of livestock – Manlay et al. (2004a)
ψ	8	-	kgN TLU ⁻¹	Quantity of N per TLU – Guerin and Roose (2015)
ν	0.5	0 - 1		Fraction of N excreted as urine – De Leeuw and Tothill (1990), Buerkert and Hiernaux (1998)
h	53	45 - 65	%	Percent of N excreted by livestock during day – Manlay et al. (2004b)
ρ	0.1	0.07 - 0.13	kgN TLU ⁻¹ day ⁻¹	Feed Requirements – De Leeuw and Tothill (1990)
K_{κ}	30	21 - 39	kgN ha ⁻¹	Monod constant demi-saturation – E.v.
g_{max}	0.5	-	day ⁻¹	Maximal grazing rate of the livestock – E.v.
ζ_{dry}	0.4	0.3 - 0.5	%	Percentage of time spend by the livestock on the bush and compound rings during the dry season, the other part being spend in savanna or corresponding to the night –E.v.
ζ_{wet}	0.2	0.15 - 0.25	%	Percentage of time spend by the livestock on fallows during the wet season, the other part of the day being spend in savanna or corresponding to the night – E.v.
b_c	1	0.7 - 1.3	-	Plant “palatability” in compound subsystem – E.v.
b_{bf}	1	0.7 - 1.3	-	Plant “palatability” in fallow subunits (bush subsystem) – E.v.
b_{bc}	0.08	0.0056 - 0.0104	-	Plant “palatability” in cropland subunits (bush subsystem) – E.v.
i_n	0.02	0.014 - 0.026	kgN ha ⁻¹ day ⁻¹	Mineral N deposition (dry and wet) – Buerkert and Hiernaux (1998), Delon et al. (2010)
i_o	0.001	0.0007 - 0.0013	kgN ha ⁻¹ day ⁻¹	Organic N deposition (dry and wet) – Buerkert and Hiernaux (1998), Delon et al. (2010)
d	0.0027	0.00189 - 0.00351	day ⁻¹	Post-fallow decomposition of woody roots – Manlay et al. (2004b)
σ	1	-	kgN ha ⁻¹	Sowing density – E.v.
λ_V	70	0 - 100	%	Recycling of household waste by village – Manlay et al. (2004b)
γ_c	10	0 - 100	%	Harvest – Manlay et al. (2004b)
γ_{bc}	60	0 - 100	%	Harvest – Manlay et al. (2004b)
δ	0.5		-	Fraction of roots from tree species in fallow plots – Manlay et al. (2004c)
ϵ	55	%	%	Harvest exported out of village – Manlay et al. (2004b)
α_b	150	0- 200	ha	Area of Bush subsystem – Manlay et al. (2004b)
α_c	50	200 - ab	ha	Area of Compound subsystem –Manlay et al. (2004b)
T	365	-	day	Number of days per annual cycle
τ	120	-	day	Number of days in the wet season
n	-	-		Index of annual cycle, number of the current year
nT^-	-	-	day	Index of the day at the beginning of the wet season before the sowing and fallow clearing

Continues on next page. . .

Param.	Value	Range (AS)	Dimensions	Description and source
nT	–	–	day	Index of the day at the beginning of the wet season after the sowing and fallow clearing
$nT + \tau^-$	–	–	day	Index of the day at the end of the dry season before the harvest
$nT + \tau$	–	–	day	Index of the day at the end of the dry season after the harvest
$\mathbb{B}02$	–	10 - 100	year	Duration of the Crop/Fallow rotation cycle and number of subunits in the bush ring
L_c	–	0 - L	year	Duration of the cropping period and number of subunits in the bush ring that are in a state of cropland
L_f	–	0 - L	year	Duration of the fallow period and number of subunits in the bush ring that are in a state of fallow

603 6.3. System of differential equations

604 All the parameters used in the model, their values, dimensions and their definitions are
605 referenced in Appendix A. Stocks and fluxes are expressed in kgN ha^{-1} and $\text{kgN ha}^{-1} \text{ day}^{-1}$,
606 respectively. The equations of the subsystems models for each season and transition event
607 during a year n are presented hereafter.

608 6.3.1. Beginning of the wet season, shifts, sowing and carrying capacity: at time nT

609 The state shifts (from fallow to cropland subunit and conversely) and the sowing are
610 discrete events that occur at time nT , at the beginning of the wet season. When they occur,
611 the following variables are updated.

612 State shifts:

613 Shifts from cropland to fallow:

$$\theta_j(t) = 0, \forall t \in [nT, (n+1)T) \text{ if } \theta_j((n-1)T) = 1 \text{ and } \theta_j((n-L_c)T) = 1$$

614 Shifts from fallow to cropland:

$$\theta_j(t) = 1, \forall t \in [nT, (n+1)T) \text{ if } \theta_j((n-1)T) = 0 \text{ and } \theta_j((n-L_c)T) = 0$$

615 In these cases, the root compartment R is also updated in the following way:

$$R_j(nT) = R_j(nT) + \delta P_j(nT)$$

616 where nT^- is the time just before nT , at the end of the dry season, before the sowing
617 and the fallow clearing.

618 *Sowing:*

619 In the compound and bush subsystems, the stock in the P compartment is initialized at
 620 a value σ (being the quantity of sown seeds expressed in kgN ha^{-1}), except for the fallow
 621 subunits of the bush subsystem that were already in the state of fallow the year before:

$$\text{Compound subsystem: } P_c(nT) = \sigma,$$

622

$$\text{Cropland subunits of the Bush subsystem: } P_j(nT) = \sigma, \forall j \text{ such that } \theta_j(nT) = 1,$$

623

$$\text{Fallow subunits of the Bush subsystem: } P_j(nT) = \sigma, \forall j \text{ such that } \theta_j(nT) = 0 \text{ and } \theta_j((n-1)T) = 1.$$

624 *Carrying capacity:*

625 In the bush subsystem

$$K_j = \begin{cases} \min(\omega I_j(nT), K_{\max}) & \text{if } \theta_j(nT) = 1 \\ K_{bf} & \text{if } \theta_j(nT) = 0 \end{cases}$$

626 6.3.2. *Wet season: from nT to $nT + \tau$*

627 In the compound subsystem:

$$\left\{ \begin{array}{l} \frac{dP_c}{dt} = \underbrace{u_c \frac{K_c - P_c}{K_c} P_c I_c}_{\text{growth}} \\ \frac{dO_c}{dt} = \underbrace{-m_c O_c}_{\text{mineralization}} + \underbrace{i_o}_{\text{atmospheric}} - \underbrace{e_{oc} O_c}_{\text{losses}} + \underbrace{\frac{\lambda_v}{\alpha_c T} V(n-1)}_{\text{recycling from dwellings}} \\ \frac{dI_c}{dt} = \underbrace{m_c O_c}_{\text{mineralization}} - \underbrace{u_c \frac{K_c - P_c}{K_c} P_c I_c}_{\text{uptake by P}} + \underbrace{i_n}_{\text{atmospheric}} - \underbrace{e_{nc} I_c}_{\text{losses}} \end{array} \right. \quad (12)$$

deposition
deposition

In the bush subsystem, for each subunit j from 1 to L :

$$\left. \begin{aligned}
 \frac{dP_j}{dt} &= \underbrace{u_j \frac{k_j - P_j}{k_j} P_j I_j}_{\text{growth}} + \underbrace{i_{pj} \frac{k_j - P_j}{k_j} P_j}_{\text{biological fixation}} - \underbrace{(1 - \theta_j) \frac{L}{\alpha_b} \phi_{wet}^j}_{\text{grazing}} \\
 \frac{dR_j}{dt} &= - \underbrace{r R_j}_{\text{degradation of R}} \\
 \frac{dO_j}{dt} &= - \underbrace{m_j O_j}_{\text{mineralization}} + \underbrace{i_o}_{\text{atmospheric}} - \underbrace{e_{oj} O_j}_{\text{losses}} + \underbrace{r R_j}_{\text{degradation of R}} + \\
 &\quad \underbrace{(1 - \theta_j) \lambda_\kappa (1 - \nu) \left(h \frac{L}{\alpha_b} \phi_{wet}^j + (1 - h) \kappa \rho \frac{L}{\alpha_b (L_f)} \right)}_{\text{deposition}} \\
 \frac{dI_j}{dt} &= \underbrace{m_j O_j}_{\text{mineralization}} - \underbrace{u_j \frac{K_j - P_j}{K_j} P_j I_j}_{\text{uptake by P}} + \underbrace{i_n}_{\text{atmospheric}} - \underbrace{e_{nj} I_j}_{\text{losses}} + \\
 &\quad \underbrace{(1 - \theta_j) \lambda_\kappa \nu \left(h \frac{L}{\alpha_b} \phi_{wet}^j + (1 - h) \kappa \rho \frac{L}{\alpha_b (L_f)} \right)}_{\text{excretion}}
 \end{aligned} \right\} \quad (13)$$

Different values are assigned to the parameters $u_j, K_j, i_{pj}, m_j, e_{oj}$ and e_{nj} depending on whether the subunit j is being cultivated during the current year or not.

$x_j = x_{bc}$ if the subunit j is cultivated or $x_j = x_{bf}$ if the subunit j lies in fallow (with $x = u, K, i_p, m, e_o$ and e_n).

6.3.3. Harvest: at time $nT + \tau$

At harvest, the plant compartment of the cultivated part of the agro-ecosystem (in the compound and bush subsystems) are updated as follows:

$$\text{Compound subsystem: } P_c(nT + \tau) = (1 - \gamma_c) P_c(nT + \tau^-)$$

$$\text{Cropland subunits of Bush subsystem: } P_j(nT + \tau) = (1 - \gamma_{bc}) P_j(nT + \tau^-), \forall j \text{ such that } \theta_j = 1$$

where $nT + \tau^-$ is the time just before $nT + \tau$, at the end of the wet season, before the harvest.

The quantity $V(n)$ of crop brought back to the dwellings after the harvest of the year n is

639 updated at this time:

$$V(n) = \underbrace{\alpha_c \gamma_c P_c(nT + \tau^-)}_{\text{from Compound subsystem}} + \underbrace{\frac{L_c}{L} \alpha_b \gamma_{bc} (1 - \epsilon) P_{bc}(nT + \tau^-)}_{\text{from cropland subunits of Bush subsystem}}$$

640 6.3.4. Dry Season: from $nT + \tau$ to $(n + 1)T$

641 In the compound subsystem:

$$\left\{ \begin{array}{l} \frac{dP_c}{dt} = - \underbrace{c_c P_c}_{\text{degradation of crop residues}} - \underbrace{\frac{1}{\alpha_c} \phi_{dry}^c}_{\text{grazing}} \\ \frac{dO_c}{dt} = \underbrace{c_c P_c}_{\text{degradation of crop residues}} - \underbrace{m_c O_c}_{\text{mineralization}} + \underbrace{i_o}_{\text{atmospheric deposition}} - \underbrace{e_{oc} O_c}_{\text{losses}} + \underbrace{\frac{\lambda_v}{\alpha_c T} V(n-1)}_{\text{recycling from dwellings}} \\ \frac{dI_c}{dt} = \underbrace{m_c O_c}_{\text{mineralization}} + \underbrace{i_n}_{\text{atmospheric deposition}} - \underbrace{e_{nc} I_c}_{\text{losses}} + \underbrace{\lambda_\kappa \nu \left(h \frac{1}{\alpha_c} \phi_{dry}^c + (1-h) \frac{\kappa \rho}{\alpha_c} \right)}_{\text{excretion}} \end{array} \right. \quad (14)$$

In the bush subsystem, for each subunit j from 1 to L :

$$\left\{ \begin{array}{l}
 \frac{dP_j}{dt} = - \underbrace{c_j P_j}_{\text{degradation of crop residues}} - \underbrace{\frac{L}{\alpha_b} \phi_{dry}^j}_{\text{grazing}} \\
 \frac{dR_j}{dt} = - \underbrace{r R_j}_{\text{degradation of R}} \\
 \frac{dO_j}{dt} = \underbrace{c_j P_j}_{\text{degradation of crop residues}} - \underbrace{m_j O_j}_{\text{mineralization}} + \underbrace{i_o}_{\text{atmospheric deposition}} - \underbrace{e_{oj} O_j}_{\text{losses}} + \underbrace{r R_j}_{\text{degradation of R}} + \underbrace{\lambda_\kappa (1 - \nu) h \frac{L}{\alpha_b} \phi_{dry}^j}_{\text{excretion}} \\
 \frac{dI_j}{dt} = \underbrace{m_j O_j}_{\text{mineralization}} + \underbrace{i_n}_{\text{atmospheric deposition}} - \underbrace{e_{nj} I_j}_{\text{losses}} + \underbrace{\lambda_\kappa \nu h \frac{L}{\alpha_b} \phi_{dry}^j}_{\text{excretion}}
 \end{array} \right. \quad (15)$$

Different values are assigned to the parameters c_j , m_j and e_{nj} depending on whether the subunit j is being cultivated during the current year or not. $x_j = x_{bc}$ if the subunit j is cultivated or $x_j = x_{bf}$ if the subunit j lies in fallow (with $x = c, m$, and e_n),

6.4. Balance of fluxes, comparison to Sare Yero Bana data

The tables 4 and 5 describe the balances of N fluxes (in kgN ha⁻¹ y⁻¹) at the scale of the compound subsystem and the bush subsystem (crops and fallow) over the last year of a 300 years simulation without and with livestock for a duration of a rotation of 20 years.

The model is designed to be simple enough to provide a mechanistic understanding of the way agricultural practices influence crop production. Therefore, it is set up to be qualitatively rather than quantitatively predictive. Yet, the comparison of the main outputs to data from Sare Yero Bana shows a rather good fit (case 1 of Table 5 presented in Appendix C, section 6.4). More precisely, N fluxes related to livestock and harvest are close to field data from Manlay et al. (2004a,b) in both the cropland subunits of the bush subsystem and the compound subsystem. On the other hand, N fluxes related to livestock in the fallow subunits

657 of the bush subsystem are of the same order of magnitude, but they are largely higher. This
658 overestimation may be mainly due to simplifying assumptions regarding livestock dynamics
659 and grazing behaviour. For instance, all the plants present in the fallows were assumed
660 palatable. In reality, fallows contain unpalatable species (Ickowicz and Mbaye, 2001), in
661 particular in late successional states, while a share of palatable biomass is left due to tainting
662 by urine and trampling during browsing (Manlay et al., 2004c). Overestimating the livestock-
663 induced fluxes in fallow tends to reduce livestock-induced fluxes from savanna, which may
664 explain the underestimation of crop production in the compound subsystem.

665 The abundance of legumes in fallows is poorly documented. Some *Acacia* spp and annual
666 legumes are present but there is no precise estimate of the amounts of N they fix. However,
667 the order of magnitude for biological N fixation fluxes ($50.4 \text{ kgN ha}^{-1} \text{ yr}^{-1}$) in our model is
668 consistent with Cleveland et al. (1999) who gave the range of value $16\text{-}44 \text{ kgN ha}^{-1} \text{ yr}^{-1}$ for
669 tropical savannas.

670 [Table 2 about here.]

671 [Table 3 about here.]

672 *6.5. Sensitivity Analysis*

673 The sensitivity analysis was performed using the Morris method that is implemented in
674 the package “sensitivity” (Pujol et al., 2017). The analysis of the Morris graph makes it
675 possible to distinguish:

- 676 • the parameters whose effects are negligible: points close to the origin (0,0);
- 677 • the parameters whose linear effect is important: points located to the right of the
678 abscissa axis;
- 679 • the parameters whose effects are non-linear or include interaction with other factors:
680 points located at the top of the y-axis (from Faivre et al., 2013).

681 The effect of each parameter of the model on the bush, the compound and the total crop
682 productions was examined. This sensitivity analysis shows that factors such as the surface
683 of the bush subsystem α_b and the size of livestock κ are among the most influential factors.
684 Some other parameters such as the harvest percentages (γ) and the plant parameter related
685 to the level of atmospheric N biological fixation in crop subunits of the bush subsystem
686 (ω) are influential too, but to a lesser extent. This result is not surprising, since these
687 parameters are directly linked to the inputs/outputs balance of the system. The importance
688 of the parameter h , which represents the percentage of N excreted by livestock during the day
689 (Manlay et al., 2004b) suggests that livestock management is a key driver in the system. It
690 calls for the consideration of other types of livestock management in future studies performed
691 with our model. For instance, in-barn livestock systems based on feed imports from outside
692 the ecosystem are practiced when landscape is dominated by crops and when rangelands
693 surfaces are insufficient to feed large livestock herds. Imported feeds represent new source of
694 N inputs that may compensate the loss of N spatial transfer from rangelands to croplands
695 (Audouin et al., 2015).

696 [Figure 7 about here.]

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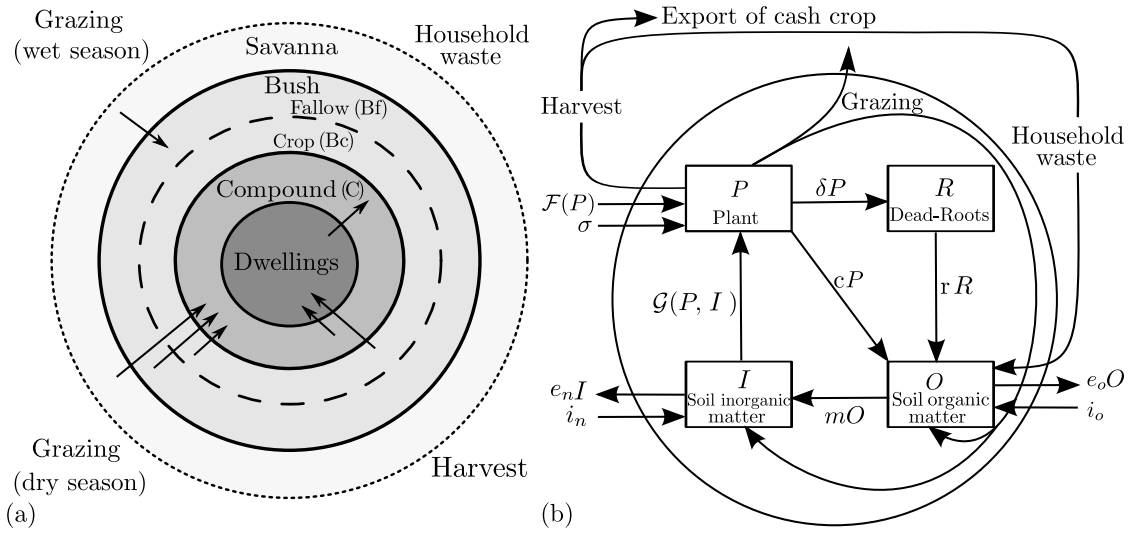


Figure 1: (a) Representation of the fluxes occurring between the rings over a year in the whole agro-ecosystem. (b) Model of the nitrogen cycle in a generic subsystem of the agro-ecosystem. Representation of all stocks and fluxes occurring over a year. See Appendix A for the description of parameters.

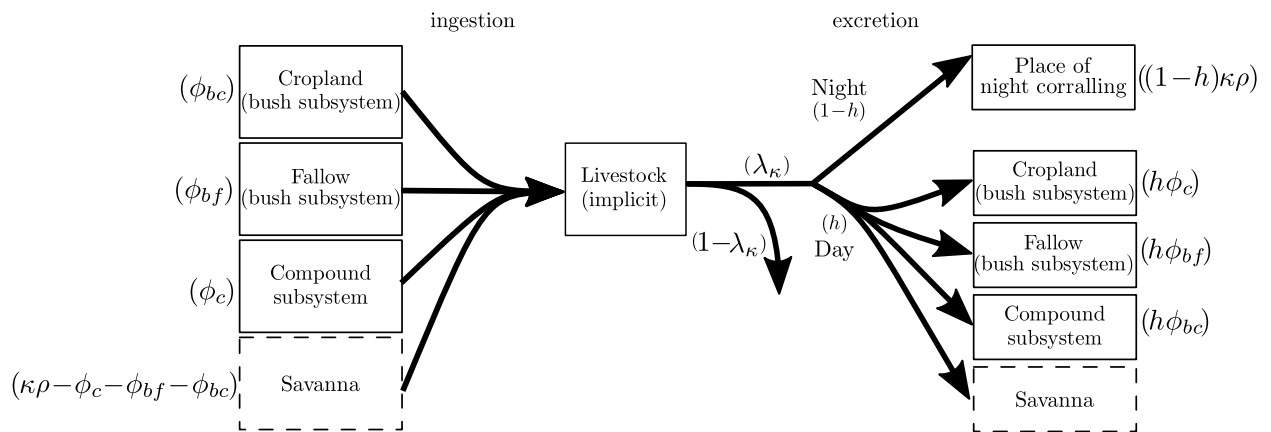
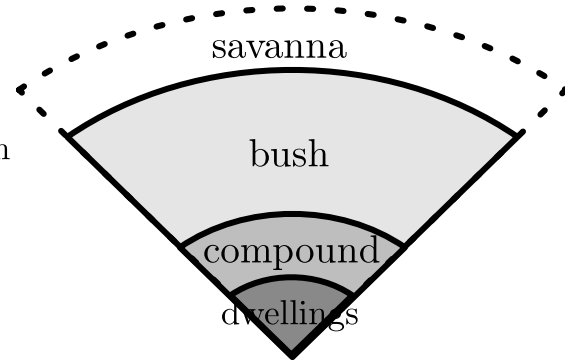
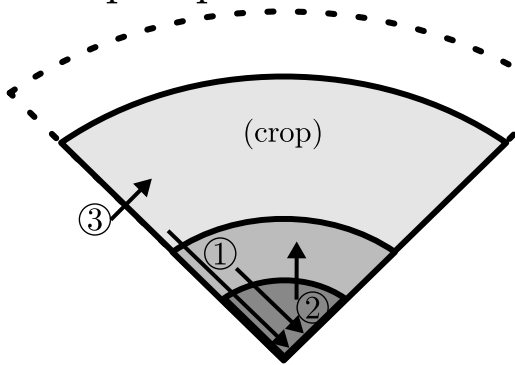


Figure 2: Representation of livestock-induced nitrogen fluxes. For the sake of simplicity, only one cropland subunit and one fallow subunit of the bush subsystem are represented. The place of night corralling is the fallow during the wet season or the compound subsystem during the dry season.

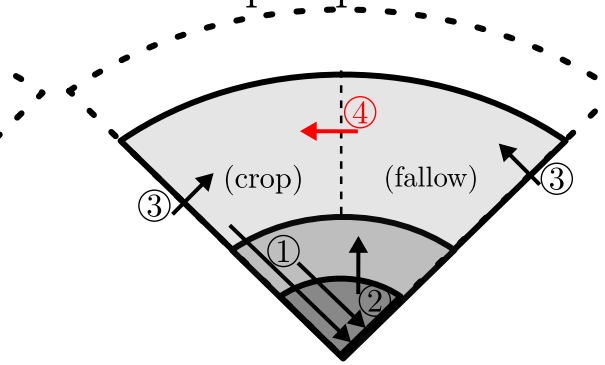
- ① Harvest
- ② Household waste
- ③ Atmospheric N biological fixation
- ④ Fallow pump
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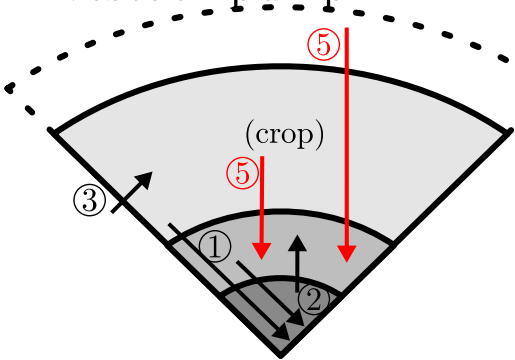
No pump



Fallow pump



Livestock pump



Both pumps

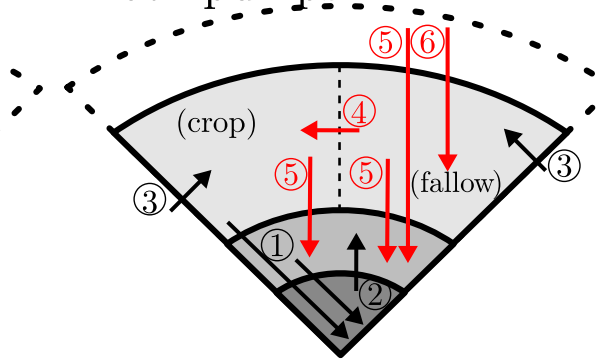


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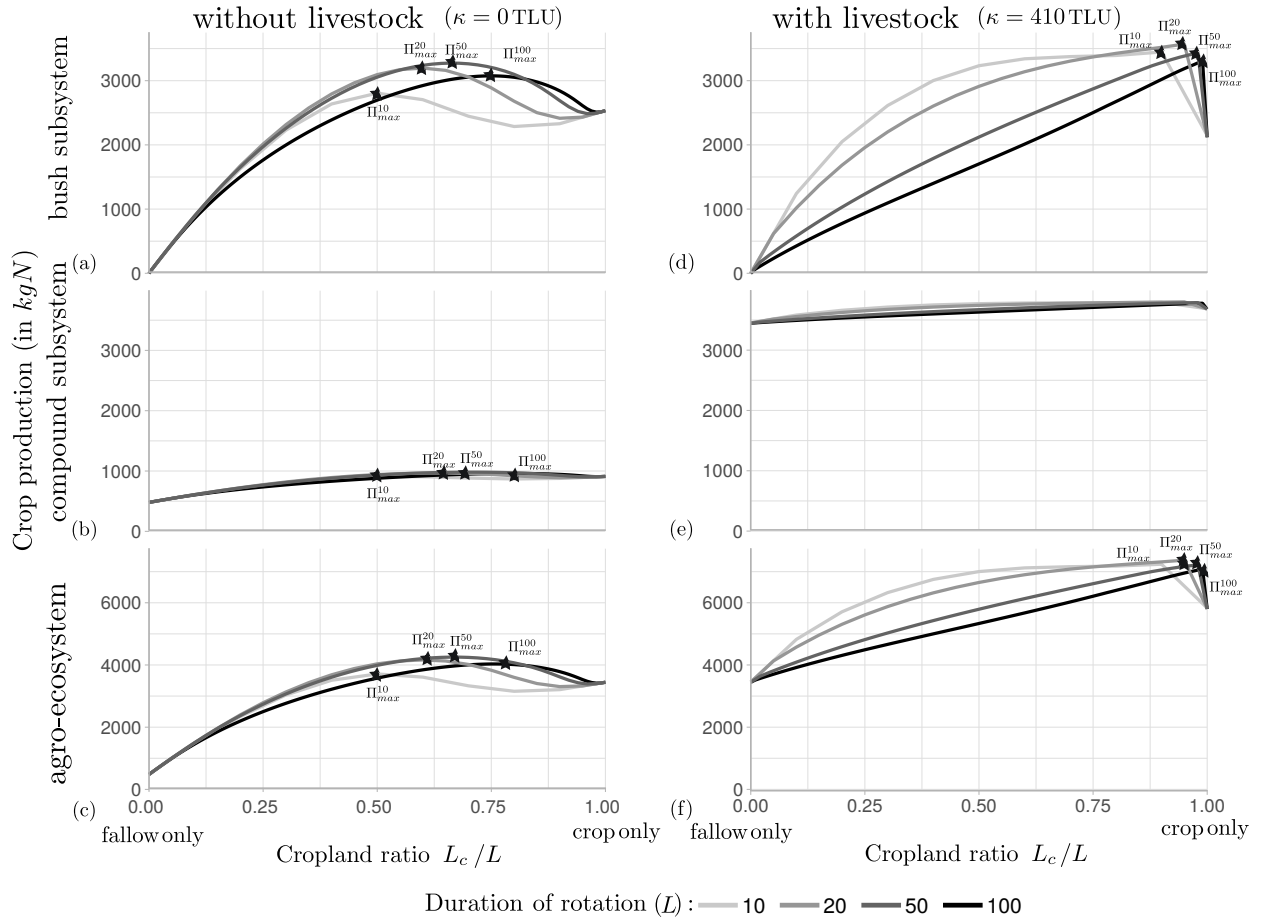


Figure 4: Crop production (in kgN) in the bush subsystem, the compound subsystem and the whole agro-ecosystem for different rotation durations and cropland ratios without (a, b and c) and with (d, e and f) livestock ($\kappa = 410$ TLU) and for a compound and bush subsystems area of 50 and 150ha, respectively. The colour of the line varies from light to dark as the duration L increases. Each line results from several simulations with different cropland ratios but a same rotation duration after 300 years of simulations. Black stars point the scenario where the maximal bush production Π_{\max} is reached for each duration of rotation (10, 20, 50 and 100 years). The crop ratio $\frac{L_c}{L}$ represents the ratio of crop duration over rotation duration. It varies from 0 (all bush subunits are fallow) to 1 (all bush subunits are crop).

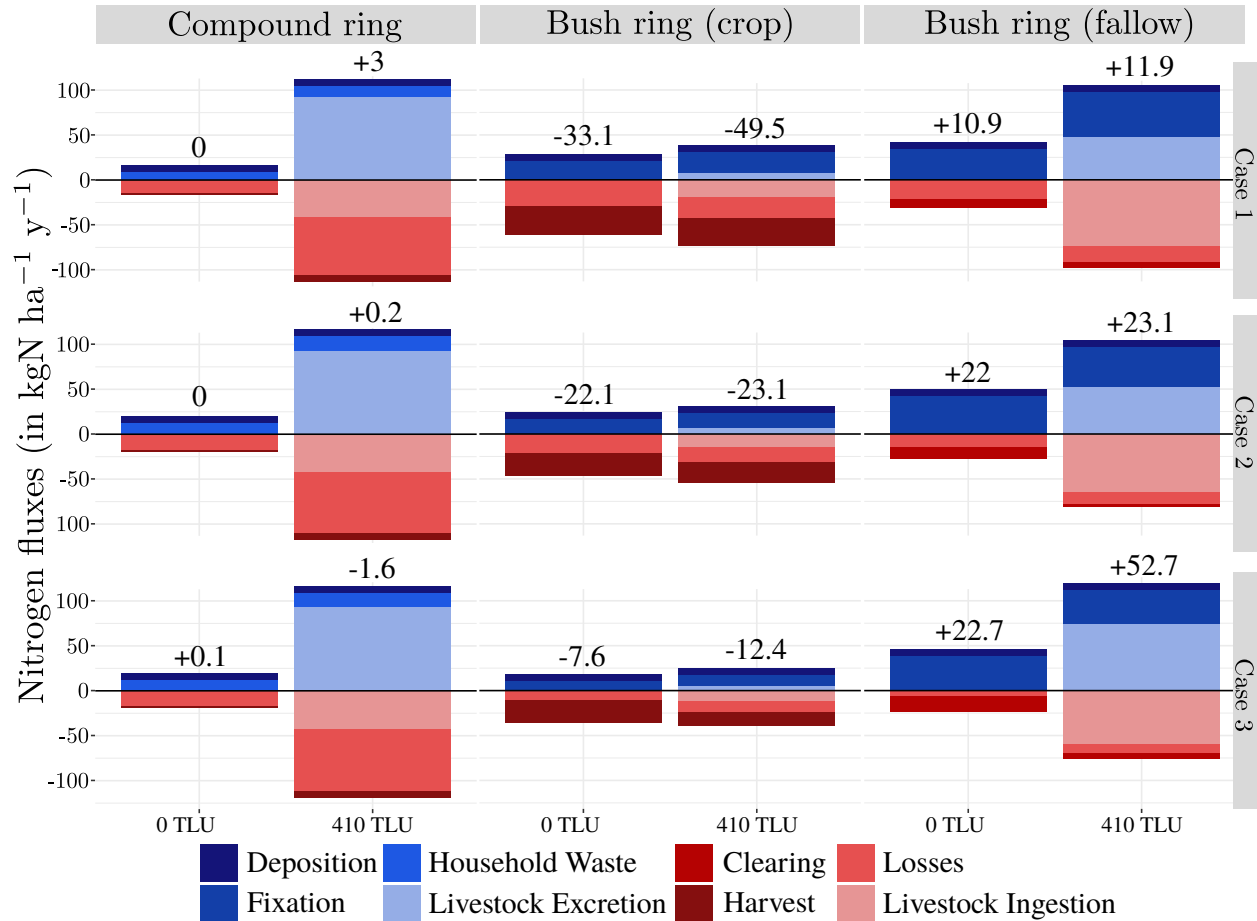


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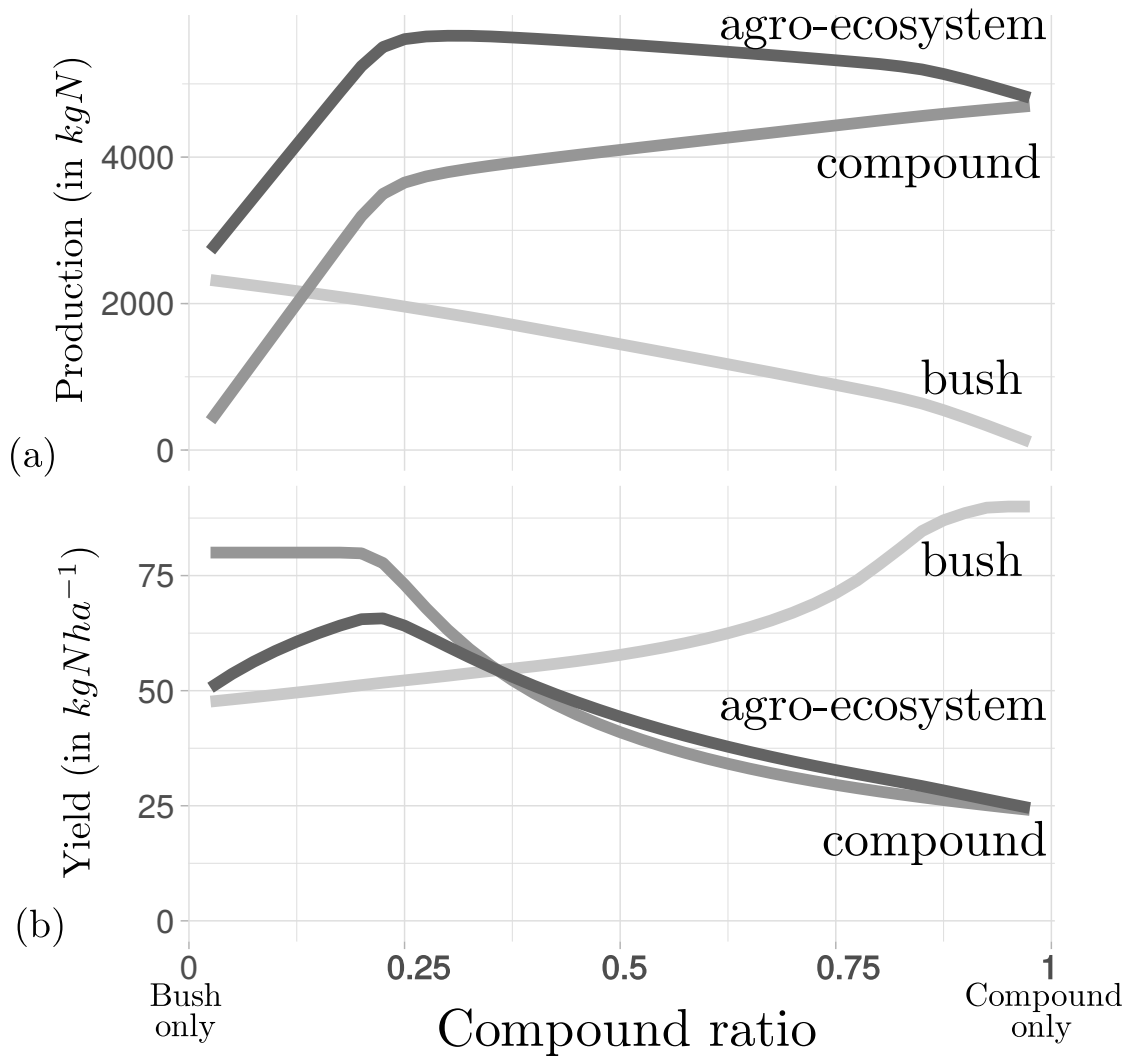


Figure 6: Crop production (in kgN) and crop yield (in kgN ha⁻¹) in bush and compound subsystems and in the whole agro-ecosystem as a function of the share of the compound subsystem in the whole agro-ecosystem. Each line results from several simulations with different cropland ratios but a same rotation duration after 300 years of simulations. The size of livestock is 410 TLU for an agro-ecosystem of 200 hectares.

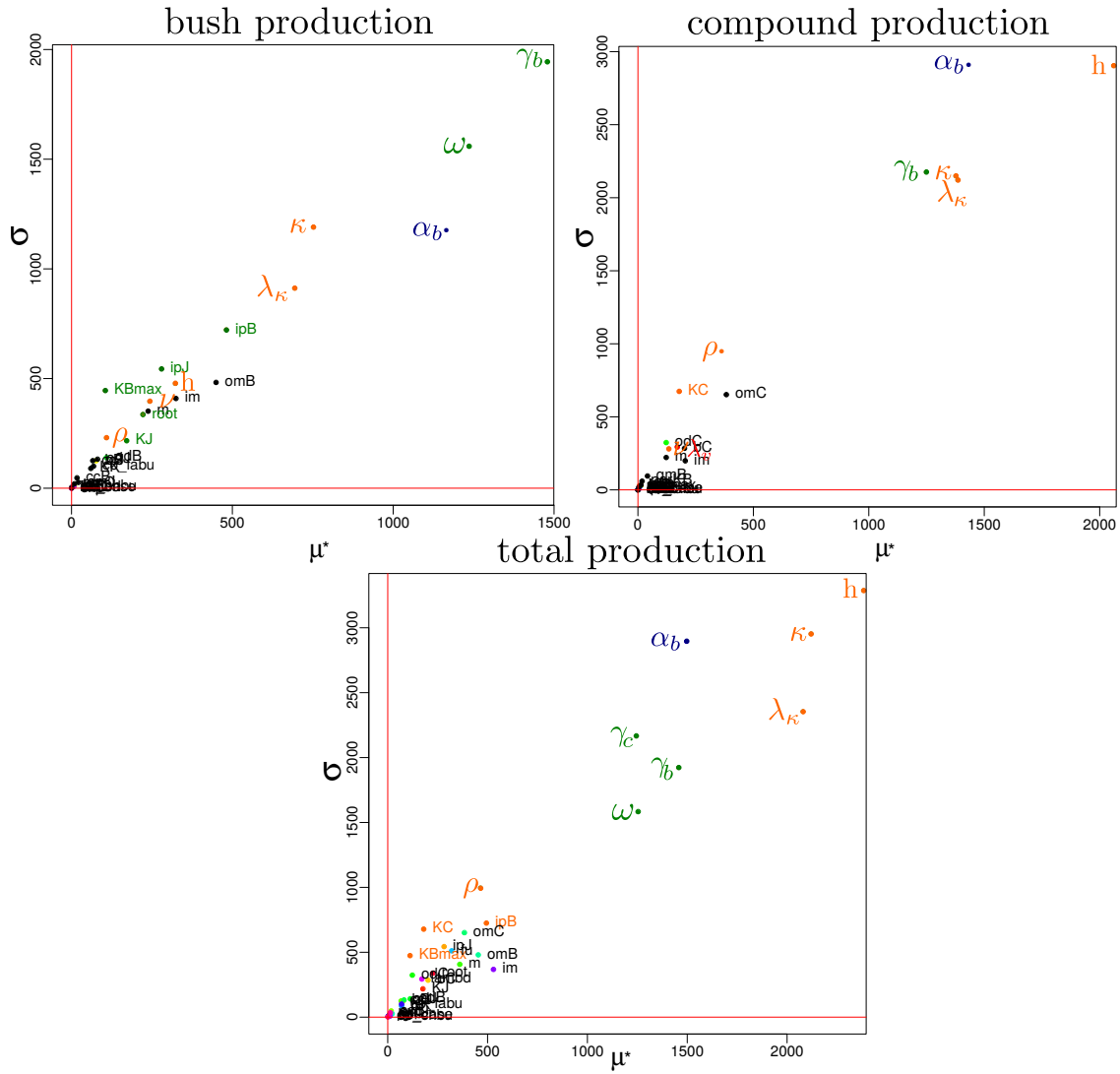


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	Rain season nT to nT + τ			Harvest at nT + τ			Dry season nT + τ to (n+1)T			Sowing/clearing at (n+1)T		
	comp.	bush		comp.	bush		comp.	bush		comp.	bush	
	crop (c)	crop (bc)	fallow (bf)	crop (c)	crop (bc)	fallow (bf)	crop (c)	crop (bc)	fallow (bf)	crop (c)	crop (bc)	fallow (bf)
harvest γ				×	×	×						
sowing σ										×	×	× ₀
fallow transfer δ											× ₁	× ₁
biological fixation i_p		×	×									
growth \mathcal{G}	×	×	×									
losses e_n	×	×	×				×	×	×			
losses e_o	×	×	×									
household waste	×						×					
degradation r		×	×					×	×			
degradation c							×	×	×			
mineralization m	×	×	×				×	×	×			
deposition i_n	×	×	×				×	×	×			
deposition i_o	×	×	×				×	×	×			
grazing			×				×	×	×			
night corralling			×				×					

Table 3: Summary of active fluxes depending on the rings and the instant in the annual cycle. Empty boxes symbolize an absence of flux, × an active flux, ×₀ and ×₁ are fluxes active during the crop/fallow and the fallow/crop shifts, respectively. c:crop; bf: bush-fallow; bc: bush-crop.

Table 4: Balance of N fluxes (in kgN ha⁻¹ y⁻¹) at the scale of the compound subsystem, bush subsystem (crops and fallow) over the last year of a 300 years simulation without livestock. In these simulations, total bush and compound areas are 150 and 50 ha, respectively. The duration of a rotation is 20 years, which corresponds to 20 plots; results in bush subsystems (crop and fallow) are a mean of plot in crop and fallow, respectively. Three cases are simulated with a different duration of cropping (5, 10 and 15 years, respectively).

Without Livestock	Compound ring		Bush ring (Crop)		Bush ring (Fallow)	
	In	Out	In	Out	In	Out
Case 1: ($L_c = 5$)						
area (ha)		50		37.5		112.5
Harvest/household waste*	8.6	1.5		32.2		0
Livestock-mediated fluxes	0	0	0	0	0	0
Losses**		14.6		29.3		21.8
Atmospheric deposition***	7.6		7.6		7.6	
Biological fixation****			21.5		34.1	
Clearing						9
Sowing	1	1.2	1	1.8		
Total	17.3	17.2	30.1	63.3	41.7	30.8
Balance		0		-33.1		10.9
Case 2: ($L_c = 10$)						
area (ha)		50		75		75
Harvest/household waste*	12.9	1.8		24.6		0
Livestock-mediated fluxes	0	0	0	0	0	0
Losses**		18.2		21.6		14.7
Atmospheric deposition***	7.6		7.6		7.6	
Biological fixation****			16.8		42.1	
Clearing						13.0
Sowing	1	1.4	1	1.4		
Total	21.5	21.4	25.4	47.5	49.7	27.7
Balance		0		-22.1		22
Case 3: ($L_c = 15$)						
area (ha)		50		112.5		37.5
Harvest/household waste*	11.7	1.7		14.8		0
Livestock-mediated fluxes	0	0	0	0	0	0
Losses**		17.2		11.4		6.9
Atmospheric deposition***	7.6	0	7.6		7.6	
Biological fixation****			10.8		39.0	
Clearing						17.0
Sowing	1	1.4	1	1.4		
Total	20.3	20.2	19.4	27.0	46.6	23.8
Balance		0.1		-7.6		22.7

*: Harvest take into account staple crop for the consumption of the village (compound ring) and exports of cash crop outside the agro-ecosystem (bush ring).

** : Losses due to erosion, leaching, volatilization and denitrification

*** : Dry and atmospheric depositions of mineral and organic N

**** : Biological fixation from N-fixing Plant association with *Rhizobium*

Table 5: Balance of N fluxes (in kgN ha⁻¹ y⁻¹) at the scale of the compound and the bush subsystem (crops and fallow) over the last year of a 300 years simulation with livestock. In these simulations, total bush and compound areas are 150 and 50 hectares, respectively. The duration of a rotation is 20 years (corresponding to 20 plots); results in bush subsystems (crop and fallow) are a mean of plots in crop and fallow, respectively. Three cases are simulated with a different duration of cropping. The case 1 represents the closest scenario of the agro-ecosystem of Sare-Yero-Bana, Senegal in 2000. Between brackets are given aggregated data calculated from (a) (Manlay et al., 2004b,a), (b) (Buerkert and Hiernaux, 1998, Delon et al., 2010), (c) Ndiaye (1986) or (d) (Cleveland et al., 1999)

With Livestock	Compound ring		Bush ring (Crop)		Bush ring (Fallow)	
	In	Out	In	Out	In	Out
Case 1: ($L_c = 5$)	50(35)		37.5(70)		112.5(117)	
area (ha)	50(35)		37.5(70)		112.5(117)	
Harvest/household waste*	12.5(63) ^a	7.3(15) ^a		31.1(56) ^a		
Livestock-mediated fluxes	92.7(146) ^a	41.3(59) ^a	8.5(12) ^a	20(21) ^a	47.8(3) ^a	74.2(7) ^a
Losses**		65.1		22.7		17.9
Atmospheric deposition***	7.6 (4-8) ^b		7.6 (4-8) ^b		7.6 (4-8) ^b	
Biological fixation****			22.3(15-68) ^c		50.3(16-44) ^d	
Clearing						6.4
Sowing	1	0.1	1			
Total	117	114	39.4	88.8	105	94
Balance		3		-49.5		11.6
Case 2: ($L_c = 10$)	50		75		75	
area (ha)	50		75		75	
Harvest/household waste*	16.1	7.5		23.1		
Livestock-mediated fluxes	93.1	42.2	6.3	14.8	51.9	64.9
Losses**		68.1		16.8		13.1
Atmospheric deposition***	7.6		7.6		7.6	
Biological fixation****			16.7		44.5	
Clearing						3.04
Sowing	1	0.1	1	0.1		
Total	117.8	117.8	31.5	54.7	104.1	81.0
Balance		0.2		-23.1		23.1
Case 3: ($L_c = 15$)	50		112.5		37.5	
area (ha)	50		112.5		37.5	
Harvest/household waste*	16.1	7.5		15.4		
Livestock-mediated fluxes	93.3	42.6	4.8	11.4	74.2	59.5
Losses**		69.6		12.2		9.7
Atmospheric deposition***	7.6		7.6		7.6	
Biological fixation****			13.1		37.8	
Clearing						6.08
Sowing	1	0.1	1	0.1		
Total	116.9	116.8	27.1	44.6	119.3	66.6
Balance		-1.6		-12.4		52.7

*: Harvest take into account staple crop for the consumption of the village (compound ring) and exports of cash crop outside the agro-ecosystem (bush ring).

*: Losses due to erosion, leaching, volatilization and denitrification

** : Dry and atmospheric depositions of mineral and organic N

***: Biological fixation from N-fixing Plant association with *Rhizobium*