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1 **Spatial heterogeneity of nitrification contributes to tree-grass**  
2 **coexistence in West African savannas**

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## 25 **Abstract**

- 26 1. In savannas, the coexistence between trees and grasses is determined by complex mechanisms  
27 based on water partitioning and disturbances. But little is known about the contribution of  
28 other resources such as N. In West African savannas, nitrification inhibition by grasses and  
29 nitrification stimulation by trees create spatial heterogeneity in nitrification fluxes and N  
30 stocks. Besides, savanna trees can also extend a part of their roots in the surrounding open  
31 area to take up N.
- 32 2. To investigate the role of the spatial heterogeneity of nitrification on tree-grass coexistence,  
33 we used a two-patch model simulating N dynamics between an open patch (without trees) and  
34 a tree clump patch (trees with grasses under their canopy). The open patch was characterized  
35 by a low nitrification rate while the tree clump patch was characterized by a high nitrification  
36 rate. Both patches were connected through horizontal fluxes due to soil horizontal exploration  
37 by tree roots. We tested coexistence for different spatial tree distributions as they are known  
38 to strongly influence savanna dynamics.
- 39 3. Our results show that the spatial heterogeneity of nitrification induces a spatial partitioning  
40 between ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ) promoting tree-grass coexistence. As  
41 nitrification inhibition by grasses leads to high  $\text{NH}_4^+$  availability in the open, the possibilities  
42 of coexistence are optimized when trees have different preferences in the open versus under  
43 their canopy. Tree-grass coexistence is thus observed when grasses prefer  $\text{NH}_4^+$ , while trees  
44 prefer  $\text{NH}_4^+$  in the open and  $\text{NO}_3^-$  under their canopy.
- 45 4. Contrary to random tree distribution, tree clumping enhances tree-grass coexistence.  
46 Intraspecific aggregation strengthens the effect of spatial heterogeneity, which decreases  
47 interspecific competition and favors tree-grass coexistence. By contrast, increasing the surface  
48 explored by tree roots in the open tends to increase tree-grass competition. This enhances the  
49 competitive ability of trees for N acquisition and consequently favors invasion by trees.

50 5. *Synthesis*. This study shows that this new coexistence mechanism based on mineral N  
51 partitioning into  $\text{NH}_4^+$  and  $\text{NO}_3^-$  can be determinant in the functioning of West African humid  
52 savannas. This mechanism probably interacts with disturbance-based mechanisms, but such  
53 interactions should be studied through new models.

54 **Keywords:**  $\text{NH}_4^+$  versus  $\text{NO}_3^-$  preference, nitrogen partitioning, nitrification, savanna, spatial  
55 heterogeneity, spatial tree distribution, tree-grass coexistence

## 56 **Introduction**

57 Savanna vegetation is characterized by a continuous layer of grasses intermixed with a discontinuous  
58 stratum of trees. The coexistence of many plant species has long been debated as it is in apparent  
59 contradiction to the principle of competitive exclusion stipulating that two species competing for the  
60 same resource cannot coexist over the long term (Hardin, 1960; Barot & Gignoux, 2004). In savannas,  
61 tree-grass coexistence has been attributed to two main causes, resource partitioning and disturbances  
62 (Sankaran et al., 2004)□. In dry savannas, the scarcity of resources, and especially water, leads to  
63 niche partitioning as grasses are more competitive than trees in the topsoil layers while trees can  
64 explore the soil vertically and take up water at greater depth (Schenk & Jackson, 2002)□. This niche  
65 differentiation through different rooting depths can favor coexistence between trees and grasses  
66 (Walter, 1971; Walker & Noy-Meir, 1982). In contrast to dry savannas, wet savannas are not limited  
67 by water and could turn into forests, but the presence of disturbances such as fire or herbivory reduces  
68 the density of trees (Sankaran et al., 2004; Staver et al., 2011)□. Fire is the main disturbance limiting  
69 woody cover by affecting the survival of tree seedlings and saplings (Gignoux et al., 2009)□. In the  
70 same way, herbivores such as grazers and browsers can have negative effects on grass and tree growth  
71 and therefore contribute to regulate the tree-grass ratio (Sankaran et al., 2008; Van Langevelde et al.,  
72 2003)□.

73 In West African savannas, the dominant perennial grass species inhibit nitrification,  
74 nitrification being the process of transformation of ammonium ( $\text{NH}_4^+$ ) into nitrate ( $\text{NO}_3^-$ ) (Lata et al.,  
75 2004; Subbarao et al. 2009; Srikanthasamy et al., 2018)□. This biological nitrification inhibition (BNI)

76 occurs through the release of grass root exudates impeding the activity of nitrifying microorganisms  
77 (Lata et al., 2004; Srikanthasamy et al., 2018). Because  $\text{NH}_4^+$  is less prone to leaching than  $\text{NO}_3^-$ ,  
78 keeping nitrogen (N) in the  $\text{NH}_4^+$  form decreases N losses by  $\text{NO}_3^-$  leaching and therefore maintains  
79 a high primary productivity (Boudsocq et al., 2009)□. By contrast, in the Lamto humid savanna (Côte  
80 d'Ivoire), the dominant tree species have been found to stimulate nitrification (Srikanthasamy et al.,  
81 2018). The mechanism explaining this stimulation is not known but one hypothesis would be that as  
82 for grasses, specific molecules from the tree root system directly impact microbial communities.  
83 Another hypothesis is that the observed increase of soil organic matter and soil humidity below tree  
84 canopy could also increase soil microorganisms activity and therefore mineralization and nitrification  
85 processes (Mordelet et al., 1993; Srikanthasamy et al., 2018)□.

86 In nutrient-limited ecosystems such as savannas, plant-soil feedbacks on N cycling can  
87 locally alter N availability (Knops et al., 2002) by creating a spatial heterogeneity in soil resources,  
88 and thereby influencing primary productivity. Trees and grasses, through their respective stimulation  
89 and inhibition strategies, could induce a resource partitioning, if grasses preferentially absorb  $\text{NH}_4^+$   
90 and trees  $\text{NO}_3^-$  promoting tree-grass coexistence in the Lamto savanna (Boudsocq et al., 2012; Konaré  
91 et al., 2019). Some studies have shown that plant preferences for different chemical N forms (organic  
92 and mineral N) can facilitate their coexistence (Ashton et al., 2010; McKane et al., 2002)□. Spatial  
93 heterogeneity due to nitrification heterogeneity could further reduce niche overlap, likely decreasing  
94 interspecific interactions and promoting coexistence of different species even on a single limiting  
95 resource (Barot & Gignoux, 2004; Chesson, 2000; Huston & DeAngelis, 1994)□. This leads to a  
96 complex picture requiring a spatially structured model to understand the consequences of plant-soil  
97 feedbacks on  $\text{NH}_4^+$  and  $\text{NO}_3^-$  availability and tree-grass coexistence.

98 Many studies highlighted the relevance of spatial patterns in ecological dynamics (Grimm  
99 et al., 1996; Grimm & Railsback, 2012). For example, intraspecific aggregation decreases the strength  
100 of interspecific competition (Pacala, 1997; Stoll & Prati, 2001), which can slow down competitive  
101 exclusion (Armstrong & McGehee, 1980)□. Spatial tree distribution is known to play an important

102 role in savanna dynamics and is strongly affected by disturbances (Menaut et al., 1990)□. In addition,  
103 tree clumps are generally considered as nutrient-rich patches (Mordelet et al., 1993) and this higher  
104 soil fertility under tree canopy is partly due to the horizontal soil exploration by tree roots in the open  
105 as it improves nutrient transfers between the open and tree clumps (Konaré et al., 2021). While spatial  
106 heterogeneity tends to foster niche partitioning (Amarasekare, 2003), horizontal fluxes can minimize  
107 the impact of this heterogeneity by homogenizing  $\text{NH}_4^+$  and  $\text{NO}_3^-$  availability between the two patches  
108 (Barot et al., 2015; Barot et al., 2014). This could thus be influential for predictions of tree-grass  
109 coexistence.

110           In contrast to the work of Konaré et al. (2019) that does not consider spatial heterogeneity  
111 (all plants explore the same N pools) and Konaré et al. (2021) that focused on the effects of spatial  
112 heterogeneity of nitrification fluxes on N fluxes and N budget, the goal of this study is to analyze the  
113 role of the spatial heterogeneity in tree-grass coexistence. To do so, we used a modified version the  
114 two-patch model previously published (Konaré et al., 2021) considering a patch of open area with a  
115 low nitrification rate and a tree clump patch with a high nitrification rate. These two patches are  
116 interconnected by horizontal fluxes (due to horizontal exploration of soil in the open area by tree  
117 roots). The novelty of this model relies on considering the relation between two model parameters  
118 (the proportion of tree roots in the open and the proportion of the savanna surface covered by tree  
119 clumps) that depends on spatial tree distribution. Using this general model, we tested the following  
120 hypotheses: (i) Compared to the mean-field model (Konaré et al., 2019), accounting for the existence  
121 of distinct N pools below and outside tree clumps fosters coexistence. (ii) Spatial heterogeneity in  
122 nitrification increases the likelihood of tree-grass coexistence with grasses preferring  $\text{NH}_4^+$  and trees  
123 preferring  $\text{NO}_3^-$  under tree canopy and  $\text{NH}_4^+$  in the open. Indeed, this spatial heterogeneity leads to a  
124 spatial niche partitioning that reduces exclusion and favors coexistence. (iii) Tree-grass coexistence  
125 depends on spatial tree distribution and is facilitated when trees are clumped. More specifically, tree  
126 clumping reduces soil exploration by tree roots in the open and thus reduces competition between  
127 trees and grasses in the open. (iv) Increasing the surface explored by tree roots in the open increases

128 horizontal fluxes between the open and the tree clump patches, which increases the competition  
129 between trees and grasses for N and consequently reduces the chances of coexistence.

## 130 **Two-patch model**

### 131 **Model description**

132 The two-patch model explores competitive interactions between trees and grasses through two  
133 patches: an open patch occupied by grasses and some tree roots (patch 1), and a tree clump patch  
134 occupied by trees with grasses growing below their canopy (patch 2) (Appendix S1). This model is a  
135 spatially explicit extension of a previously published mean-field model (Konaré et al., 2019). The  
136 model tracks N dynamics between plant compartments: grass biomass ( $G_1$ ) in the open and, grass  
137 ( $G_2$ ) and tree ( $T$ ) biomass in the tree clump patch, and soil compartments: soil organic matter ( $O$ ),  
138 ammonium ( $N_A$ ) and nitrate ( $N_N$ ) in both patches (see Fig. 1, Konaré et al., 2021). Spatial  
139 heterogeneity due to nitrification inhibition (BNI) by grasses and nitrification stimulation by trees is  
140 represented by a low nitrification rate in the open ( $n_1$ ) and a high nitrification rate under tree clumps  
141 ( $n_2$ ). Both patches are interconnected through horizontal fluxes due to the ability of trees to extend  
142 horizontally their roots to take up nutrients in the open. In the model, N is supposed to be the limiting  
143 factor of primary production and grass and tree growth depend on the acquisition of mineral N forms,  
144 that can be acquired under two forms ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) with a certain preference ( $\beta$ ) for  $\text{NH}_4^+$  versus  
145  $\text{NO}_3^-$ . This preference ranges between 0 and 1 with high values of  $\beta$  corresponding to a high  
146 preference for  $\text{NH}_4^+$ . N is absorbed by plants through N uptake rates  $\beta u$  for  $\text{NH}_4^+$  uptake and  $(1-\beta) u$   
147 for  $\text{NO}_3^-$  uptake. Plants release N into organic N pool at constant mortality rates  $d_G$ ,  $d_l$  and  $d_r$ ,  
148 respectively for grasses, tree leaves and tree roots. Organic N mineralized into  $\text{NH}_4^+$  at rate  $m$  and  
149  $\text{NH}_4^+$  can be transformed into  $\text{NO}_3^-$  at rate  $n$ . Each patch receives N inputs through dry and wet  
150 depositions that provide N under organic and mineral forms into  $O$ ,  $N_A$  and  $N_N$  compartments  
151 respectively at rates  $i_O$ ,  $i_{N_A}$  and  $i_{N_N}$ . Non-symbiotic fixation contributes to the input of  $\text{NH}_4^+$  and is  
152 included in  $i_{N_A}$  (Abbadie, 2006). N losses from savannas result from the burning of the plant  
153 compartments ( $l_G$  and  $l_T$ ), and leaching for other compartments ( $l_O$ ,  $l_{N_A}$  and  $l_{N_N}$ ).  $\text{NO}_3^-$  losses by

154 **denitrification are included in  $l_{NN}$ .** All parameters but nitrification rates are equal between the two  
 155 patches to keep the model relatively simple and focus on the effects of nitrification heterogeneity (see  
 156 model parameter Table, Appendix S2). All compartments are N stocks expressed as a quantity of N  
 157 by surface unit, i.e kilograms of N per hectare of savanna ( $\text{kg N ha}^{-1}$ ). The system of differential  
 158 equations is the same used in Konaré et al. (2021):

159 Open patch (patch 1)

$$160 \quad \frac{dG_1}{dt} = (1 - \gamma)(\beta_G u_G N_{A1} G_1 + (1 - \beta_G) u_G N_{N1} G_1 - (d_G + l_G) G_1) \quad (1)$$

$$161 \quad \frac{dO_1}{dt} = (1 - \gamma)\left(i_O + d_G G_1 + d_r \left(\frac{\gamma}{1 - \gamma}\right) \alpha r T - (m + l_O) O_1\right) \quad (2)$$

$$162 \quad \frac{dN_{A1}}{dt} = (1 - \gamma)\left(i_{NA} + m O_1 - \left(\beta_G u_G G_1 + n_1 + l_{NA} + \beta_{T1} u_r \left(\frac{\gamma}{1 - \gamma}\right) \alpha r T\right) N_{A1}\right) \quad (3)$$

$$163 \quad \frac{dN_{N1}}{dt} = (1 - \gamma)\left(i_{NN} + n_1 N_{A1} - \left((1 - \beta_G) u_G G_1 + l_{NN} + (1 - \beta_{T1}) \left(\frac{\gamma}{1 - \gamma}\right) u_r \alpha r T\right) N_{N1}\right) \quad (4)$$

164 Tree clump patch (patch 2)

$$165 \quad \frac{dG_2}{dt} = \gamma (\beta_G u_G N_{A2} G_2 + (1 - \beta_G) u_G N_{N2} G_2 - (d_G + l_G) G_2) \quad (5)$$

$$166 \quad \frac{dT}{dt} = \gamma (1 - \alpha) (\beta_{T2} u_r N_{A2} r T + (1 - \beta_{T2}) u_r N_{N2} r T) + \alpha$$

$$167 \quad (\beta_{T1} u_r N_{A1} r T + (1 - \beta_{T1}) u_r N_{N1} r T) - (d_l (1 - r) + d_r \alpha r + (1 - \alpha) d_r r + l_T) T$$

168 (6)

$$169 \quad \frac{dO_2}{dt} = \gamma (i_O + d_G G_2 + (1 - \alpha) d_r r T + d_l (1 - r) T - (m + l_O) O_2) \quad (7)$$

$$170 \quad \frac{dN_{A2}}{dt} = \gamma (i_{NA} + m O_2 - (\beta_G u_G G_2 + (1 - \alpha) \beta_{T2} u_r r T + n_2 + l_{NA}) N_{A2}) \quad (8)$$

$$171 \quad \frac{dN_{N2}}{dt} = \gamma (i_{NN} + n_2 N_{A2} - ((1 - \beta_G) u_G G_2 + l_{NN} + (1 - \beta_{T2})(1 - \alpha) u_r r T) N_{N2}) \quad (9)$$

## 172 **Spatial setting of the model**

173 The description of the spatial setting in the model relies on the proportion of tree roots in the open ( $\alpha$ )  
 174 and the proportion of the savanna surface covered by tree clumps ( $\gamma$ ) (leaving  $(1 - \gamma)$  to the open  
 175 savanna). Compared to Konaré et al. (2021) in which  $\alpha$  and  $\gamma$  had fixed values, in this version of the  
 176 model,  $\alpha$  is a function of  $\gamma$  and  $\gamma$  is a function of tree biomass ( $T$ ). We assume that  $\alpha$  depends on the  
 177 proportion of tree cover and the spatial patterns of trees: for a given canopy and root system radius,



178  $\alpha$  should decrease with  $\gamma$ . However, this relation should also depend on tree distribution with lower  
179 values of  $\alpha$  when trees are clumped and high values of  $\alpha$  when they are randomly or regularly  
180 distributed. Although tree distribution can vary in different savanna ecosystems, it is often clustered  
181 (Barot et al., 1999; Gignoux et al., 2006). Similarly, we assume a positive relationship between  $\gamma$  and  
182 tree biomass  $T$ : the more trees, the more surface they occupy in savanna.

183         The shape of the relation between  $\alpha$  and  $\gamma$  was studied by simulating different distributions  
184 of trees (random, clustered and regular). We assumed that trees were represented as two superimposed  
185 discs describing the canopy and the root system as the majority of tree roots has been found within a  
186 radius 10 m away from tree clump center (Menaut, personal communication). In our simulations,  
187 canopy radius was set to 2 m and root system radius to 6 m. The relation between  $\alpha$  and  $\gamma$  was obtained  
188 by calculating the proportion of root system that did not fall under the canopy of other trees for each  
189 tree distribution and for different tree densities exploring a wide range of tree cover. We calculated  
190 the relation between  $\alpha$  and  $\gamma$  for random, clumped and regular tree distributions. To simulate random  
191 patterns, a Poisson process with a tree density varying from 1 to 100 trees ha<sup>-1</sup> by step of 10 and from  
192 100 to 2000 trees ha<sup>-1</sup> by step of 200 was used. Clumped patterns were obtained by using a Matérn  
193 cluster process (Matérn, 1960) with a tree density varying from 1 to 100 trees ha<sup>-1</sup> by step of 10 and  
194 from 100 to 1000 trees ha<sup>-1</sup> by step of 100 with a mean clump radius of 2 m and a mean number of  
195 trees per clump of 10. Finally, regular patterns were modeled using a Matérn hard-core process  
196 (Matérn, 1960; 1986) with an inhibition distance of 2 m and the same tree densities as the random  
197 patterns. To determine the relation between  $\alpha$  and  $\gamma$ , and between  $\gamma$  and  $T$ , we calculated the quantity  
198 of tree roots outside tree canopy at the individual scale and the mean of all individual values to obtain  
199  $\alpha$  for a given tree density. We then calculated  $\gamma$  for each tree density by determining the total space  
200 occupied by trees. Linear regression models were then used to determine the relation between  $\alpha$  and  
201  $\gamma$ . Besides, we used data from Menaut & César (1979) to establish the relation between  $\gamma$  and tree  
202 biomass ( $T$ ) through a linear regression model. Equations from linear models and parameters were  
203 included in the two-patch model to link  $\alpha$ ,  $\gamma$  and  $T$ .

## 204 **Model analysis and parameterization**

205 The analysis of the model relied on numerical simulations as it could not be analytically solved. All  
206 simulations were coded in R (R development Core Team, 2022) using deSolve package for the  
207 resolution of differential equations (Soetart et al., 2010). All simulations were run for 3000 years,  
208 which was sufficient to reach steady states for all compartments.

209 We used the same parameter sets as in Konaré et al. (2021; see Appendix S2) but run a  
210 completely different simulation experiment. These parameters are based on data from the Lamto  
211 savanna in Côte d'Ivoire (06°13'N, 05°02'W) (Abbadie et al., 2006) (Appendix S2).

212 Tree-grass coexistence was determined using the mutual invasibility criterion (Chesson & Ellner,  
213 1989). This criterion considers a pair of invader and resident species (for example grasses invading a  
214 forest, starting with a negligible biomass of 0.01 kg N/ha compared to the tree biomass, with a high  
215 biomass of 10 kg N/ha, and then the reverse situation with trees invading a grassland). When the two  
216 species are able to invade each other, they are assumed to mutually coexist over the long term  
217 (Chesson & Ellner, 1989). Nitrification stimulation under tree clumps suggests a preference of trees  
218 for  $\text{NO}_3^-$  at least for roots under the tree canopy. Because  $\text{NH}_4^+$  should be the dominant N form in the  
219 open due to nitrification inhibition by grasses, a preference of trees for  $\text{NH}_4^+$  in the open is more  
220 expected. We thus decided to distinguish the preference of trees for  $\text{NH}_4^+$  versus  $\text{NO}_3^-$  in the open  
221 patch ( $\beta_{TI}$ ) and under tree clumps ( $\beta_{T2}$ ) and tree preference under tree clumps was fixed to a constant  
222 value ( $\beta_{T2} = 0.25$ ). Simulations of N stocks and fluxes were performed for different combinations of  
223 grass and tree preference for  $\text{NH}_4^+$  versus  $\text{NO}_3^-$  in the open ( $\beta_G$  and  $\beta_{TI}$ ) varying between 0 and 1 with  
224 an increment of 0.005. We first simulated mutual invasion between trees and grasses for different  
225 combinations of grass and tree preference for  $\text{NH}_4^+$  versus  $\text{NO}_3^-$  (tree preference was the same in the  
226 open and under tree canopy:  $\beta_T$ ) versus different combinations of grass and tree preferences for  $\text{NH}_4^+$   
227 versus  $\text{NO}_3^-$  in the open ( $\beta_{TI}$ ) to compare the effect of tree preference on tree-grass coexistence.  
228 Nitrification rates in the open and under tree clumps were calculated by dividing nitrification fluxes  
229 under grasses and under trees by their respective ammonium stocks (Srikanthasamy et al., 2018). We

230 increased the nitrification rate in the open to compare a spatial homogeneity to a spatial heterogeneous  
231 nitrification rate to test the importance of heterogeneity in nitrification flux on tree-grass coexistence.  
232 Moreover, because the proportion of tree roots in the open does not depend only on tree density or  
233 biomass, but also on the spatial distribution of individual trees, we tested the effects of tree  
234 distributions in space (random, regular and clustered) on tree-grass coexistence. We tested the  
235 sensitivity of results to the root radius by increasing this radius from 6 to 12 m to assess the  
236 relationship between  $\alpha$  and  $\gamma$  and then analyze the effect of these new equations on tree-grass  
237 coexistence.

## 238 **Results**

### 239 **Links between soil exploration by tree roots and tree cover and between tree biomass and tree** 240 **cover**

241 For all spatial distributions tested, a negative linear relation was observed between  $\alpha$  and  $\gamma$  (p-value  
242  $< 0.0001$  and  $R^2 = 0.999$  for random and regular; p-value  $< 0.0001$  and  $R^2 = 0.996$  for cluster tree  
243 pattern) (Fig. 1a). As expected, the relation yields lower  $\alpha$  values in the case of clustered trees  
244 compared to random and regular distribution. The regression lines whereas follow:  $\alpha = -0.897\gamma +$   
245  $0.889$ ,  $\alpha = -0.872\gamma + 0.890$  and  $\alpha = -0.698\gamma + 0.694$  respectively for random, regular and clustered  
246 tree patterns. We observe a significant difference between cluster and random or regular patterns but  
247 the difference between random and regular patterns was not significant. Fig. 1b shows that  $\gamma$   
248 significantly increases with tree biomass (p-value  $< 0.005$ ,  $R^2 = 0.962$ ), which leads to  $T = 530.56\gamma -$   
249  $2.81$ . Despite the potential nonlinearity between  $\gamma$  and  $T$ , we chose to use a linear relationship in our  
250 model for simplicity. We used these results to parameterize simulations testing for tree-grass  
251 coexistence.

### 252 **Tree-grass coexistence is affected by tree preference for $\text{NH}_4^+$ in the open versus under tree** 253 **canopy**

254 Model simulation for clustered tree distribution leads to three cases of coexistence: (1) a case where  
255 trees and grasses are spatially separated (no grasses under trees, only in the open hereafter called tree-

256 grass mosaic), (2) a case where grasses can only grow under tree clumps (no open area) hereafter  
257 called savanna woodland, and (3) a case where grasses grow both under tree canopy and in the open  
258 (hereafter called savanna). When tree preference is the same in the open and under tree canopy (Fig.  
259 2a), grasses successfully invade and exclude trees for a large range of grass preference for  $\text{NH}_4^+$   
260 versus  $\text{NO}_3^-$  and when trees prefer  $\text{NO}_3^-$ . Tree-grass mosaic occurs when grasses have a higher  
261 preference for  $\text{NH}_4^+$  than trees ( $0 < \beta_T < 0.8$ ). By contrast, when tree preference for  $\text{NH}_4^+$  is higher than  
262 grasses, trees completely invade and exclude grasses. We also observe a small portion of the  
263 parameter space where tree clumps establish when grasses prefer  $\text{NO}_3^-$  and trees strongly prefer  $\text{NH}_4^+$   
264 ( $\beta_T > 0.98$ ). Savanna tree-grass coexistence is possible when grasses have a high preference for  $\text{NH}_4^+$   
265 and trees prefer  $\text{NO}_3^-$  and when grasses have a higher preference for  $\text{NH}_4^+$  than trees ( $0 < \beta_T < 0.3$ ).

266 If trees have different preferences in the open ( $\beta_{T1}$  ranged between 0 and 1) versus under  
267 tree canopy ( $\beta_{T2}$  constant) (Fig. 2b), the sizes of the zone of savanna woodland and savanna strongly  
268 increases while the zone of tree-grass mosaic decreases. Savanna is favored for a large range of tree  
269 preference in the open ( $\beta_{T1}$ ) and a grass preference for  $\text{NH}_4^+$ . Tree clumps establishment becomes  
270 possible when grasses and trees in the open prefer  $\text{NH}_4^+$ . Taken together, a same tree preference in the  
271 open and under tree canopy reduces possibilities of complete coexistence between trees and grasses  
272 but favors tree-grass mosaic, while different tree preference in the open and under tree canopy  
273 increases possibilities of coexistence between trees and, grasses in the open and under tree canopy.  
274 We thus consider different tree preference in the open versus under tree canopy for all other  
275 simulations.

### 276 **Tree-grass coexistence depends on spatial tree distribution**

277 Because results of regular and random tree distribution are virtually the same (Appendix S5), we only  
278 presented clustered and random distribution in the main text. Tree distribution strongly influences the  
279 conditions of coexistence between trees and grasses (Fig. 3). For random tree distribution, grasses  
280 invade and exclude trees when grasses have a higher preference for  $\text{NH}_4^+$  than trees in the open ( $\beta_{T1}$   
281  $< 0.4$ ). However, when tree roots in the open have a higher preference for  $\text{NH}_4^+$  than grasses ( $\beta_G <$

282 0.7), trees successfully invade and exclude grasses. The model also predicts a zone in which savanna  
283 establishes when  $\beta_G > 0.7$  and  $0.4 < \beta_{TI} < 0.73$ , a zone where tree clumps invade when grasses and  
284 trees in the open prefer  $\text{NH}_4^+$  and a small zone of tree-grass mosaic.

285 Compared to random tree distribution, clustered pattern strongly increases the size of the  
286 zones of savanna and tree-grass mosaic. Tree-grass mosaic is enhanced when the grass preference for  
287  $\text{NH}_4^+$  is higher than the tree preference for  $\text{NH}_4^+$  in the open ( $\beta_{TI}$ ). Savanna zone extends to large range  
288 of  $\beta_{TI}$  values and a preference of grasses for  $\text{NH}_4^+$ . Switching from random to clustered tree  
289 distribution also reduces the size of the zone of invasion by grasses or by trees or by savanna  
290 woodland (Appendix S3).

### 291 **Comparison between spatial heterogeneity and spatial homogeneity cases**

292 Spatial heterogeneity of nitrification due to its control by plants alters conditions of coexistence  
293 between trees and grasses. We compared the case of spatial heterogeneity (Fig. 3) to a case of spatial  
294 homogeneity where grasses do not inhibit nitrification (Fig. 4). In the case of a random tree  
295 distribution, increasing nitrification rate in the open promotes invasion by tree clumps ( $\beta_G > 0.69$  and  
296  $\beta_{TI} > 0.35$ ) or by trees only ( $\beta_G < 0.69$  and for all combinations of  $\beta_{TI}$ ). Compared to cases where  
297 nitrification is spatially heterogenous (Fig. 3), we observed a zone of tree-grass mosaic for  $0.4 < \beta_G$   
298  $< 0.62$  and  $\beta_{TI} < 0.13$  and a zone of savanna when grasses prefer  $\text{NH}_4^+$  ( $\beta_G > 0.62$ ) and trees prefer  
299  $\text{NO}_3^-$  in the open ( $\beta_{TI} < 0.28$ ) in the spatial homogeneity case. For a clustered tree distribution, the  
300 overall pattern is virtually the same, but a second zone of tree-grass mosaic appears when grasses and  
301 trees in the open strongly prefer respectively  $\text{NO}_3^-$  ( $\beta_G < 0.2$ ) and  $\text{NH}_4^+$  ( $\beta_{TI} > 0.95$ ). Increasing  
302 nitrification rate reduces total coexistence between trees and grasses and facilitates zones with only  
303 trees or trees with grasses under their canopy. This shows that different nitrification rates in the open  
304 and in the tree clump patch improve chances of tree-grass coexistence.

### 305 **Soil exploration by tree roots affects tree-grass coexistence**

306 Fig. 5 displays the outcome of mutual invasion between trees and grasses when the tree root system  
307 radius is increased from 6 m to 12 m. As described above, savanna (grasses grow both under tree

308 canopy and in the open) in random distribution cases occurs when  $\beta_G > 0.7$  and  $0.4 < \beta_{TI} < 0.73$  and  
309 the size of this zone increases and extends to more combinations of  $\beta_{TI}$  when we switch from a random  
310 to a clustered tree distribution (root radius = 6 m, Figs 5a and b). We observe the same tendencies  
311 when the root radius is increased to 12 m (Appendix S4). Overall, clustered distributions tend to  
312 increase the size of the savanna zone. However, increasing the surface explored by tree roots reduces  
313 the sizes of the zone of tree-grass coexistence in cases of both random and clustered distributions  
314 (Figs 5c and 5d). This is more perceptible for clustered patterns for which the size of the savanna and  
315 tree-grass mosaic zones largely decreases while the zone of invasion by grasses increases (Fig. 5d).

## 316 **Discussion**

317 In our model, tree-grass coexistence occurs when plants have contrasted preferences for  $\text{NH}_4^+$  versus  
318  $\text{NO}_3^-$ . This is in agreement with theories showing that the coexistence of different species is possible  
319 when they differ in their use of resources (Armstrong & McGehee, 1980). This is also in agreement  
320 with published works on competition for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  between plants (Boudsocq et al., 2012;  
321 Konaré et al., 2019). These results are also supported by empirical studies on N partitioning indicating  
322 that plant having different preferences for different chemical N forms can coexist (Ashton et al., 2010;  
323 McKane et al., 2002)□. Mineral N partitioning appears as a stabilizing mechanism (Chesson, 2000;  
324 Barot & Gignoux, 2004) fostering coexistence between savanna trees and grasses. Here, we further  
325 analyze the influences of these processes on tree-grass coexistence testing for the effects of spatial  
326 heterogeneity in nitrification fluxes (hypothesis 1), mineral N partitioning into  $\text{NH}_4^+$  and  $\text{NO}_3^-$   
327 (hypothesis 2), spatial tree patterns (hypothesis 3) and horizontal soil exploration by tree roots  
328 (hypothesis 4).

## 329 **Comparison between the one-patch and the two-patch model**

330 Compared to the mean-field model (Konaré et al., 2019), the two-patch model allows to simulate  
331 distinct pools of mineral N available below tree clumps and in the open. Although the sizes of the  
332 zone of savanna in the two-patch model (cluster distribution, Fig. 3) and in the mean-field model (Fig.  
333 2A, Konaré et al. (2019)) are not significantly different, the two-patch model predicts different

334 possible cases of coexistence that corresponds to different landscape structures. Indeed, while the  
335 mean-field model only allows one possible case of tree-grass coexistence, the two-patch model can  
336 lead to three types of coexistence: savanna woodland (trees with grasses under their canopy only),  
337 tree-grass mosaic (trees with grasses only in the open) or savanna (trees with grasses everywhere).  
338 These results are in accordance with theories showing that coexistence in a spatially heterogeneous  
339 environment is facilitated (Chesson, 2000; Amasekare, 2003) even with a single resource. In this case,  
340 spatial heterogeneity separates the mineral N resource so that this resource is no longer fully shared  
341 between the competitors leading to more diverse scenarios of coexistence in the two-patch than in the  
342 one-patch model.

### 343 **Heterogeneity in nitrification influences tree-grass coexistence in the Lamto savanna**

344 Studies on resource-based mechanisms of tree-grass coexistence in savannas have focused on water  
345 competition (Walter, 1971; Walker & Noy-Meir, 1982). Little is known, however, about other  
346 resources that are essential for plant growth, such as N (Donzelli et al., 2013)□. In our model, when  
347 trees have the same preference in the open and under tree canopy, savannas occur when grasses have  
348 a high preference for  $\text{NH}_4^+$  and trees a high preference for  $\text{NO}_3^-$  (Fig. 2). This confirms that tree-grass  
349 coexistence is possible when grasses prefer  $\text{NH}_4^+$  and trees prefer  $\text{NO}_3^-$  at least under tree canopy.  
350 Wang and Macko (2011) studied the preference of grasses depending on climatic conditions and  
351 found that grasses tend to prefer  $\text{NH}_4^+$  in humid areas. Moreover, ongoing studies on *Hyparrhenia*  
352 *diplandra* in the Lamto savanna (Barot, personal communication) as well as a study on *Andropogon*  
353 *gayanus* (Rossiter-Rachor et al., 2009)□ suggest that these two species that inhibit nitrification, have  
354 a preference for  $\text{NH}_4^+$ . Unlike the mean-field model where trees and grasses coexist when grasses  
355 prefer  $\text{NO}_3^-$  and trees prefer  $\text{NH}_4^+$  (Konaré et al., 2019), in the two-patch model, tree-grass coexistence  
356 becomes possible when grasses prefer  $\text{NH}_4^+$  and trees prefer  $\text{NO}_3^-$ . This is more in accordance with  
357 the Lamto savanna case as grasses are known to inhibit nitrification while trees stimulate it (Lata et  
358 al., 2004; Srikanthasamy et al., 2018). The N limitation in the Lamto savanna (Abbadie et al., 2006)

359 has induced the evolution of different strategies: a conservative strategy for grasses through the BNI  
360 capacity and an acquisitive strategy for trees through nitrification stimulation (Barot et al., 2015)□.

361 Konaré et al. (2021) showed that  $\text{NH}_4^+$  uptake by tree roots outside tree canopy (35.58%  
362 of total N uptake by trees) increased tree biomass. Our results confirm this scenario because different  
363 tree preference for  $\text{NH}_4^+$  versus  $\text{NO}_3^-$  in the open and under tree canopy (trees prefer  $\text{NH}_4^+$  in the open  
364 and  $\text{NO}_3^-$  under their canopy) increases the zone of savanna, i.e. tree-grass coexistence (Fig. 2).  
365 Besides, simulations testing different values of tree preference for  $\text{NH}_4^+$  versus  $\text{NO}_3^-$  under their  
366 canopy showed that increasing tree preference for  $\text{NH}_4^+$  under tree canopy reduces the establishment  
367 of savanna zones but promotes tree invasion (Appendix S6). These results suggest that plasticity of  
368 tree root systems in their preferences for  $\text{NH}_4^+$  versus  $\text{NO}_3^-$  should occur depending on the spatial  
369 distribution of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  (Britto & Kronzucker, 2013)□. In both cases (same versus different  
370 tree preferences), our results show that local interactions between species and their environment can  
371 induce a spatial heterogeneity leading to niche partitioning and thus promote their coexistence  
372 (Huston & DeAngelis, 1994; Amasekare, 2003). These different impacts of trees and grasses on  
373 nitrification create small-scale heterogeneities by increasing the availability of their preferred N form,  
374 which induces niche complementarity for N acquisition. In comparison, increasing nitrification rate  
375 in the open reduces coexistence and favors the establishment of zones with only trees and savanna  
376 woodland (Fig. 4). Indeed, increasing this rate reduces heterogeneity in nitrification which increases  
377 niche overlap (Chesson, 2000; Amasekare, 2003) and increases the competitive ability of trees for N.  
378 Taken together, these feedbacks based on N recycling tend to stabilize the open and tree clump  
379 patches and to favor tree-grass coexistence at a larger scale. Besides, the preference for  $\text{NH}_4^+$  versus  
380  $\text{NO}_3^-$  qualitatively influences savanna dynamics, confirming that this preference can have important  
381 consequences at the ecosystem scale on vegetation dynamics (Boudsocq et al., 2012) and  
382 quantitatively on plant biomass (Appendix S7). While plasticity in plant preference for  $\text{NH}_4^+$  versus  
383  $\text{NO}_3^-$  has already been described, our results suggest that we should acquire experimental results to



384 measure this preference on savanna trees and its spatial variability and to analyze the underlying  
385 mechanisms along Britto and Kronzucker's arguments (Britto & Kronzucker, 2013).

### 386 **Tree spatial distribution alters the conditions of coexistence**

387 Many modeling studies have demonstrated that species coexistence could be facilitated by  
388 intraspecific clustered distributions (Inouye, 1999; Hartley & Shorrocks, 2002). Our results confirm  
389 that coexistence is easier when trees are clumped than when they are randomly distributed. In a  
390 random tree distribution, grass and tree roots growing outside tree canopy easily overlap in the open.  
391 This increases competitive interactions between trees and grasses for N acquisition in the open  
392 through lateral N exchanges following the horizontal soil exploration by tree roots. The strong  
393 competition between trees and grasses in the open prevents the establishment of tree-grass mosaic  
394 and savanna zones whereas it facilitates invasions by grasses or by trees depending on their  
395 preferences for  $\text{NH}_4^+$  versus  $\text{NO}_3^-$ . By contrast, the clumping of trees limits the proportion of tree  
396 roots in the open as tree individuals are surrounded by more conspecifics (tree roots tend to be more  
397 under the canopy of neighbouring trees). This decreases transfers of N between the open and the tree  
398 clump patch through horizontal fluxes and highlights the impact of spatialization: intraspecific  
399 aggregation tends to foster intraspecific competition over interspecific competition. Some studies  
400 found that intraspecific aggregation is influential for species coexistence as it facilitates the  
401 maintenance of weaker competitors (Stoll & Prati, 2001; Monzeglio & Stoll, 2005). Taken together,  
402 tree spatial patterns influence the outcomes of competition by impacting the strength of intra relative  
403 to interspecific competition (Stoll & Prati, 2001). Besides, in some savannas (Couteron & Kokou,  
404 1997; Skarpe, 1991) and particularly in the Lamto savanna (Barot et al., 1999; Gignoux et al.,  
405 2006), trees often show an aggregated spatial distribution. They form clumps leaving an important  
406 proportion of the surface covered by grasses. Tree clumps are maintained by fires: reduced grass  
407 biomass under tree shading decreases fire intensity and hence increases tree sapling survival  
408 (Hochberg et al., 1994; Gignoux et al., 2006). This mechanism somehow increases the likelihood of  
409 tree-grass coexistence by impeding fires (promoted by grass biomass) to kill all tree saplings. **Our**

410 results suggest that tree clumps may favor tree-grass coexistence and savanna maintenance through  
411 another mechanism: a decrease in the competition for mineral N, but empirical studies are needed to  
412 support this effect of tree spatial distribution on savanna dynamics.

### 413 **The impact of horizontal soil exploration on coexistence**

414 Horizontal soil exploration contributes to nutrient enrichment under tree canopy (Konaré et al., 2021)  
415 but little is known about their possible effects on coexistence. Our results show that regardless of tree  
416 distribution, savanna and tree-grass mosaic zones are reduced by the increase of the surface explored  
417 by tree roots. Indeed, horizontal soil exploration by tree roots leads to spatial transfers of N between  
418 the open and the tree clump patches. Increasing the proportion of tree roots in the open increases the  
419 competitive ability of trees to take up N and thus the competition between trees and grasses for N in  
420 the open. Although, cluster distribution allows a spatial partitioning by increasing intraspecific  
421 competition, this proliferation of tree roots in the open increases the strength of interspecific  
422 competition relative to intraspecific competition (Stoll & Prati, 2001) and consequently prevents grass  
423 establishment. These lateral fluxes between these two patches lowers the spatial heterogeneity by  
424 homogenizing the N availability between these two patches (Barot et al., 2015; Barot et al., 2014),  
425 which tends to reduce complete coexistence and favors the zones of exclusion by trees and by grasses  
426 (Appendix S3). Moreover, when the size of the tree root system relative to the canopy increases, the  
427 relation between the proportion of tree roots in the open and tree cover is virtually the same for each  
428 distribution (Appendix S4). As a result, increasing the surface explored by tree roots decreases the  
429 differences between random and clustered tree distribution.

### 430 **Conclusion**

431 Savanna ecosystems can be viewed as small scale meta-ecosystems (Loreau et al., 2003) where the  
432 spatial heterogeneity in nitrification between the two patches and the intensity of lateral N fluxes  
433 strongly influences the outcomes of competition between trees and grasses. Our findings confirm that  
434 spatial heterogeneity in nitrification promotes tree-grass coexistence when trees and grasses have  
435 different preference for  $\text{NH}_4^+$  versus  $\text{NO}_3^-$  with grasses preferring  $\text{NH}_4^+$  and trees  $\text{NO}_3^-$  under their

436 canopy. While increasing the soil exploration by tree roots in the open tends to increase the  
437 competitive ability of trees to acquire N, intraspecific aggregation through cluster tree distribution  
438 intensifies the effect of spatial heterogeneity, which lowers the competition between trees and grasses  
439 favoring their coexistence. Mineral N partitioning into  $\text{NH}_4^+$  and  $\text{NO}_3^-$  can play an important role by  
440 promoting tree-grass coexistence. Although the ability to inhibit nitrification seems to be common in  
441 African perennial grasses and some crops (Lata et al., 2004; Subbarao et al., 2009; Rossiter-Rachor  
442 et al., 2009, O'Sullivan et al., 2016; Lata et al. 2022), little is known about environmental conditions  
443 that have selected for this behavior (but see Lata et al. (2022)). Even if this inhibition has not been  
444 assessed in other savanna types, mineral N partitioning could be involved in the tree-grass coexistence  
445 of all West African humid savannas that have virtually the same dominant grass and tree species as  
446 Lamto savanna. The high performance of African grasses and their effects on N cycling in northern  
447 Australian and South American savannas (D'Antonio & Vitousek, 1992; Rossiter-Rachor et al., 2009)  
448 also seem to be linked to their BNI ability. Though the frequency of this ability in other African  
449 grasses is not fully known (Lata et al., 2022), many African grasses seem to be able to inhibit  
450 nitrification so that the new coexistence mechanism we emphasize should be studied at a large  
451 geographical scale and particularly in Eastern and Southern African savannas. Besides, N fixing trees  
452 and large herbivores, that are absent in the Lamto savanna, are known to be influential in the  
453 functioning of other savannas such as East African savannas (Sankaran et al., 2008). These  
454 mechanisms, that provide important N inputs through symbiotic fixation, animal dungs and urine and  
455 impact N cycling differently, should be included in new models to assess the robustness of our results.

456         Clearly, our new mechanism of coexistence based on the partition of the mineral N  
457 resource, probably interacts with formerly identified mechanisms based on the impact of disturbances  
458 on tree demography to explain tree-grass coexistence (Higgins et al., 2000). Although fire is  
459 determinant for the maintenance of savanna structure by reducing woody cover (Gignoux et al., 2006),  
460 mineral N partitioning likely acts in interaction with fire as the intensity of fire depends on the  
461 biomass of flammable grasses, this grass biomass depending in turn on their N acquisition, essential

462 nutriment for their growth. For instance, nitrification inhibition by grasses has been shown to increase  
463 grass biomass, which should increase fire intensity and its capacity to impede tree encroachment.  
464 This would ultimately favor tree-grass coexistence. However, new models should be built to take into  
465 account mechanisms based on both resource competition and demography.

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## 472 **Conflict of interest statement**

473 The authors declare no conflict of interest.

## 474 **Author contributions**

475 SK, KFK, S Bo, JG, JCL, XR and S Ba conceived the ideas and designed methodology. SK analyzed  
476 the model and wrote the manuscript with the contribution of all co-authors. All authors gave final  
477 approval for publication.

## 478 **Data availability statement**

479 All data regarding the model is included in the paper.

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645 **List of figures**

646 **Figure 1:** (a) Proportion of tree roots in the open ( $\alpha$ ) as a function of tree cover ( $\gamma$ ) according to  
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 652 ( $\beta_T$ ). (b): trees have different preferences for  $\text{NH}_4^+$  in the open ( $\beta_T$ ) and the tree patch ( $\beta_{T2}$ ). In these  
 653 simulations,  $\beta_{T2}$  was set constant to 0.25. Simulations correspond to clustered tree distributions.  
 654 Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T:  
 655 tree-grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland  
 656 (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence  
 657 between trees and grasses under their canopy and in the open).

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659 **Figure 3:** Mutual invasibility plots between trees and grasses according to random (a) and clustered  
 660 (b) tree distributions at the savanna scale. Invasion zones: G1+G2: grasses invade and exclude trees,  
 661 T: Trees invade and exclude grasses, G1+T: tree-grass mosaic (coexistence between trees and grasses  
 662 in the open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy),  
 663 G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

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665 **Figure 4:** Mutual invasibility plots between trees and grasses according to random (a) and clustered  
 666 (b) tree distributions at the savanna scale. These figures correspond to cases where grasses do not  
 667 inhibit nitrification (spatial homogeneity:  $n_1 = n_2 = 4.16 \text{ yr}^{-1}$ ). Invasion zones: G1+G2: grasses invade  
 668 and exclude trees, T: Trees invade and exclude grasses, G1+T: tree-grass mosaic (coexistence

669 between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and  
670 grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their  
671 canopy and in the open)

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673 **Figure 5:** Mutual invasibility plots between trees and grasses according to random (a and c) and  
674 clustered (b and d) tree distributions at the savanna scale. The first (a and b) and second (c and d)  
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676 of 6 and 12 m when determining the relation between  $\alpha$  and  $\gamma$ . Invasion zones: G1+G2: grasses invade  
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678 between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and  
679 grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their  
680 canopy and in the open).

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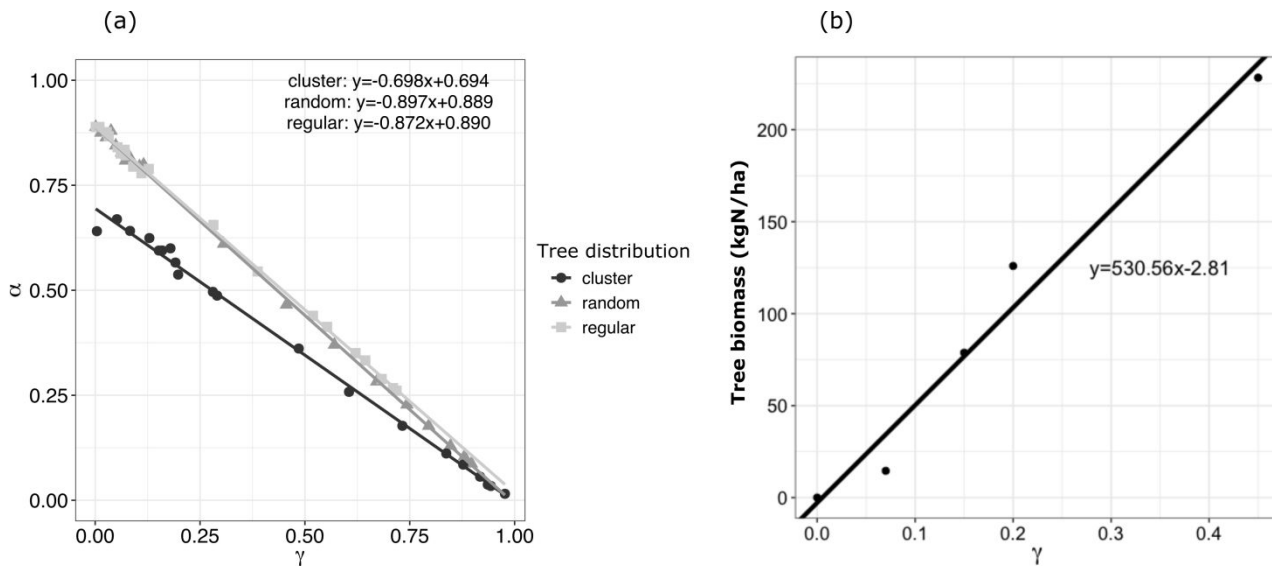
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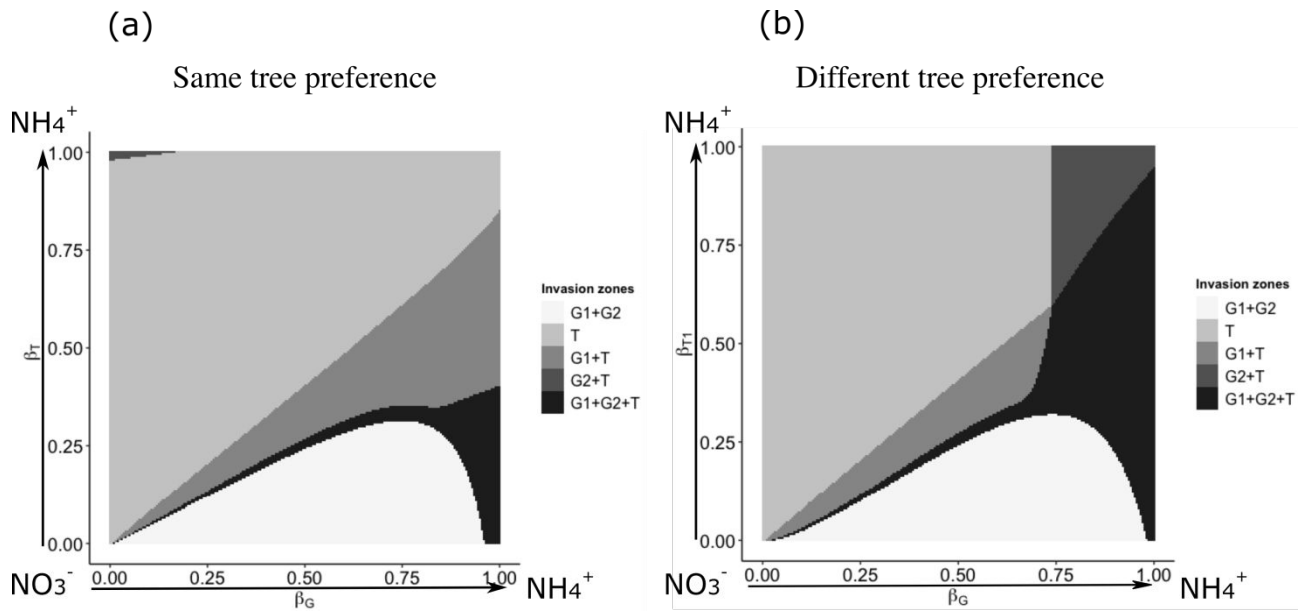
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Fig. 1

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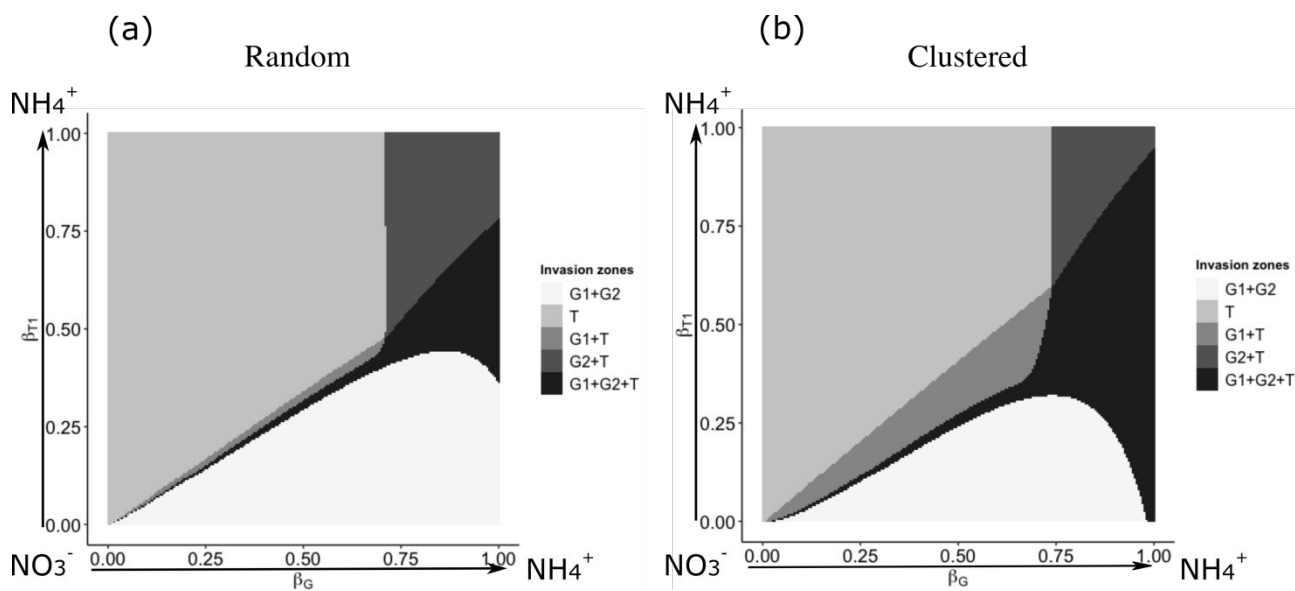
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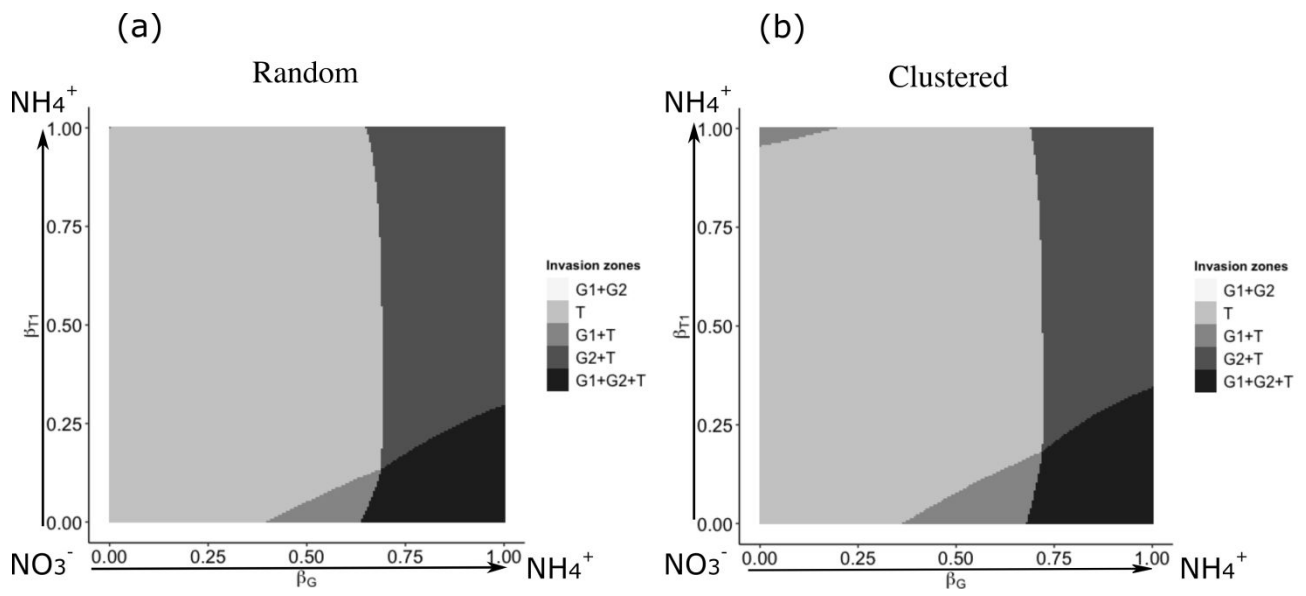
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Fig. 2



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Fig. 3



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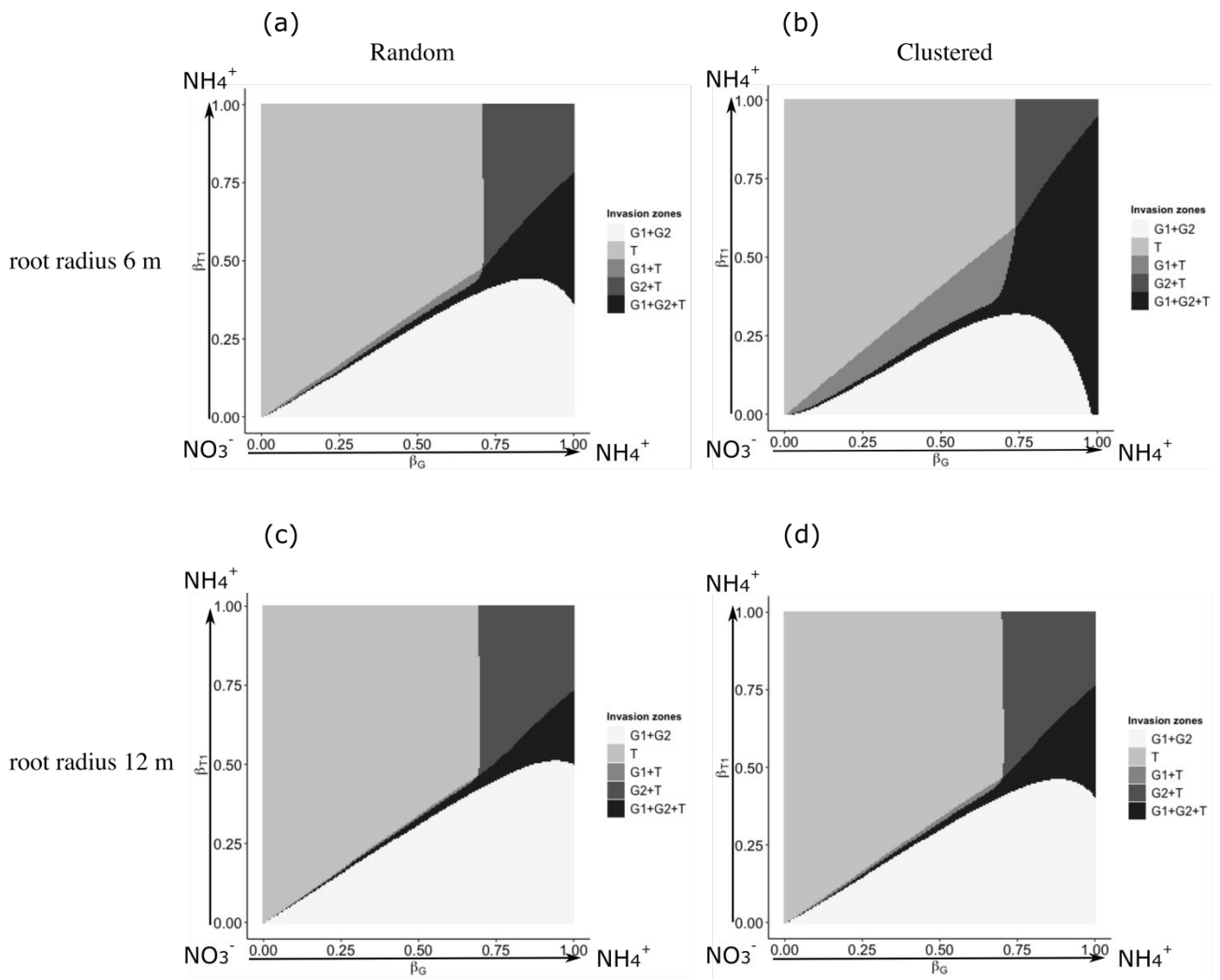
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Fig. 4



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Fig. 5

1 **Supporting information**

2 **Appendix S1: Schematic representation of the two-patch model**

3 **Appendix S2: Model parameters**

4 **Appendix S3: Graphical representation of scenarios of invasion by trees versus invasion by**  
5 **grasses**

6 **Appendix S4: Relation between soil exploration by tree roots and tree cover**

7 **Appendix S5: Regular distribution**

8 **Appendix S6: Effect of tree preference under their canopy depending on spatial tree**  
9 **distributions**

10 **Appendix S7: Plant biomass depending on tree distributions**

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12 **Figure S1:** Schematic representation of the two-patch model showing the patchy vegetation of the  
13 Lamto savanna with the open patch only occupied by grasses and the tree clump patch with trees and  
14 grasses beneath their canopy.

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16 **Table 1:** Model parameters

17

18 **Figure S3-a:** Two-patch model representing N dynamics between the open patch and the tree clump  
19 patch. This figure displays a scenario of invasion by trees resulting from the two-patch model  
20 simulation for cluster tree distribution. Red lines correspond to fluxes strongly influenced by the  
21 invasion by trees while black lines the fluxes less influenced by the invasion by trees.

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23 **Figure S3-b:** Two-patch model representing N dynamics between the open patch and the tree clump  
24 patch. This figure displays a scenario of invasion by grasses resulting from the two-patch model  
25 simulation for cluster tree distribution. Red lines correspond to fluxes strongly influenced by the  
26 invasion by grasses while black lines the fluxes less influenced by the invasion by grasses.

27 **Figure S4:** Proportion of tree roots in the open ( $\alpha$ ) as a function of tree cover ( $\gamma$ ) according to cluster,  
28 random and regular tree distribution for a root radius equals to 12 m.

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30 **Figure S5-a:** Mutual invasibility plots between trees and grasses according to grass ( $\beta_G$ ) and tree  
31 ( $\beta_{TI}$ ) preference for  $\text{NH}_4^+$  in the open patch at the savanna scale. Simulations corresponds to regular  
32 tree distribution with cases of spatial homogeneity ( $n_1 = n_2 = 4.16 \text{ yr}^{-1}$ ) (left) and cases of spatial  
33 heterogeneity ( $n_1 \neq n_2$ ) (right). Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees  
34 invade and exclude grasses, G1+T: tree-grass mosaic (coexistence between trees and grasses in the  
35 open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy),  
36 G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

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38 **Figure S5-b:** Mutual invasibility plots between trees and grasses according to grass ( $\beta_G$ ) and tree  
39 ( $\beta_{TI}$ ) preference for  $\text{NH}_4^+$  in the open patch at the savanna scale. The graph corresponds to simulations  
40 of regular tree distributions with a root system radius of 6 m (left) and 12 m (right) when determining  
41 the relation between  $\alpha$  and  $\gamma$ . Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees  
42 invade and exclude grasses, G1+T: tree-grass mosaic (coexistence between trees and grasses in the  
43 open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy),  
44 G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

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46 **Figure S6:** Mutual invasibility plots between trees and grasses according to random (left) and  
47 clustered (right) tree distributions at the savanna scale. The preference of trees under tree canopy  
48 increases from the top to the bottom and corresponds respectively to  $\beta_{T2}=0.25$ ;  $\beta_{T2}=0.35$  and  $\beta_{T2}=0.5$ .  
49 Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T:  
50 tree-grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland  
51 (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence  
52 between trees and grasses under their canopy and in the open).

53

54 **Figure S7-a:** Grass (patterns a and b) and tree (patterns c and d) biomass as a function of grass ( $\beta_G$ )  
55 and tree ( $\beta_{TI}$ ) preference for  $\text{NH}_4^+$  in the open according to random tree distributions at the savanna  
56 scale.

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58 **Figure S7-b:** Grass (patterns a and b) and tree (patterns c and d) as a function of grass ( $\beta_G$ ) and tree  
59 ( $\beta_{TI}$ ) preference for  $\text{NH}_4^+$  in the open patch according to clustered tree distributions at the savanna  
60 scale.

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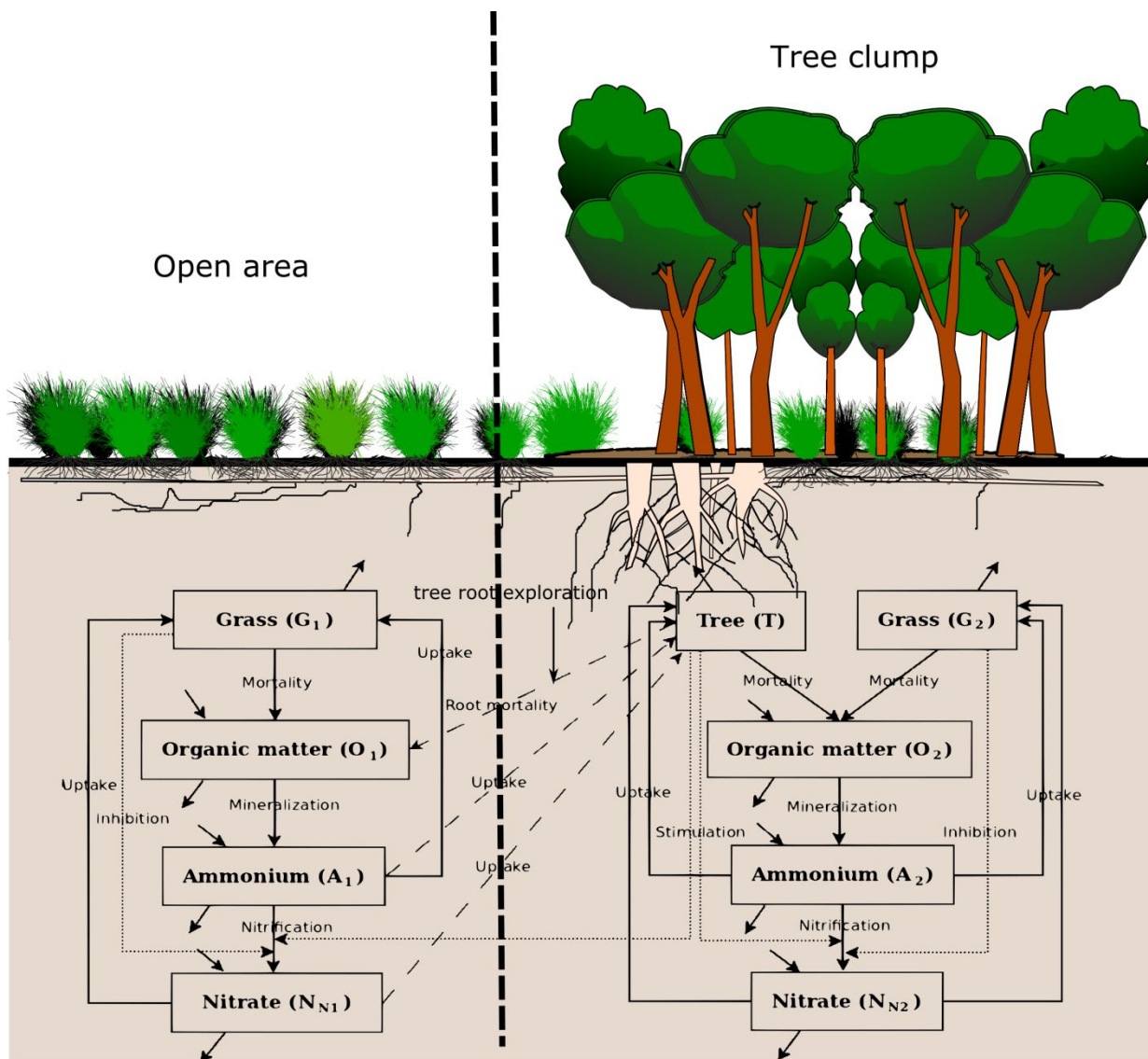
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80 **Appendix S1: Schematic representation of the two-patch model**

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86 **Figure S1**

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92 **Appendix S2: Model parameters**

93 Table 1: Model parameters

Parameters	Definition	Unit	Values
Grass parameters			
$d_G$	Turnover rate of grass	yr <sup>-1</sup>	0.6
$l_G$	Rate of N losses from grass compartment	yr <sup>-1</sup>	0.4
$u_G$	N uptake rate	ha kg <sup>-1</sup> N yr <sup>-1</sup>	0.14186
$\beta_G$	Preference for NH <sub>4</sub> <sup>+</sup>	No unit	-
Tree parameters			
$d_r$	Turnover rate of tree roots	yr <sup>-1</sup>	0.08
$d_l$	Turnover rate of tree leaves	yr <sup>-1</sup>	0.073
$l_T$	Rate of N losses from tree compartment	yr <sup>-1</sup>	0.11
$u_r$	N uptake rate by tree roots	ha kg <sup>-1</sup> N yr <sup>-1</sup>	0.08
$\beta_{T1}$	Preference for NH <sub>4</sub> <sup>+</sup> in the open patch	No unit	-
$\beta_{T2}$	Preference for NH <sub>4</sub> <sup>+</sup> in the tree clump patch	No unit	0.25
$\alpha$	Fraction of roots in the open	No unit	-
$\gamma$	Tree clumps proportion	No unit	-
$r$	Root shoot ratio	No unit	0.5
Soil parameters			
$i_O$	N organic input to the savanna	kg N ha <sup>-1</sup> yr <sup>-1</sup>	16.5
$m$	N mineralization rate	yr <sup>-1</sup>	0.025
$l_O$	N loss from the N organic compartment in surface soil layer	yr <sup>-1</sup>	0.0027
$i_{NA}$	NH <sub>4</sub> <sup>+</sup> inputs to the savanna	kg N ha <sup>-1</sup> yr <sup>-1</sup>	23
$n_1$	Nitrification rate in the open patch	yr <sup>-1</sup>	0.09
$n_2$	Nitrification rate in the tree clump patch	yr <sup>-1</sup>	4.16
$l_{NA}$	NH <sub>4</sub> <sup>+</sup> loss rate	yr <sup>-1</sup>	0.0133
$i_{NN}$	NO <sub>3</sub> <sup>-</sup> inputs to the savanna	kg N ha <sup>-1</sup> yr <sup>-1</sup>	4.1
$l_{NN}$	NO <sub>3</sub> <sup>-</sup> loss rate	yr <sup>-1</sup>	2.7

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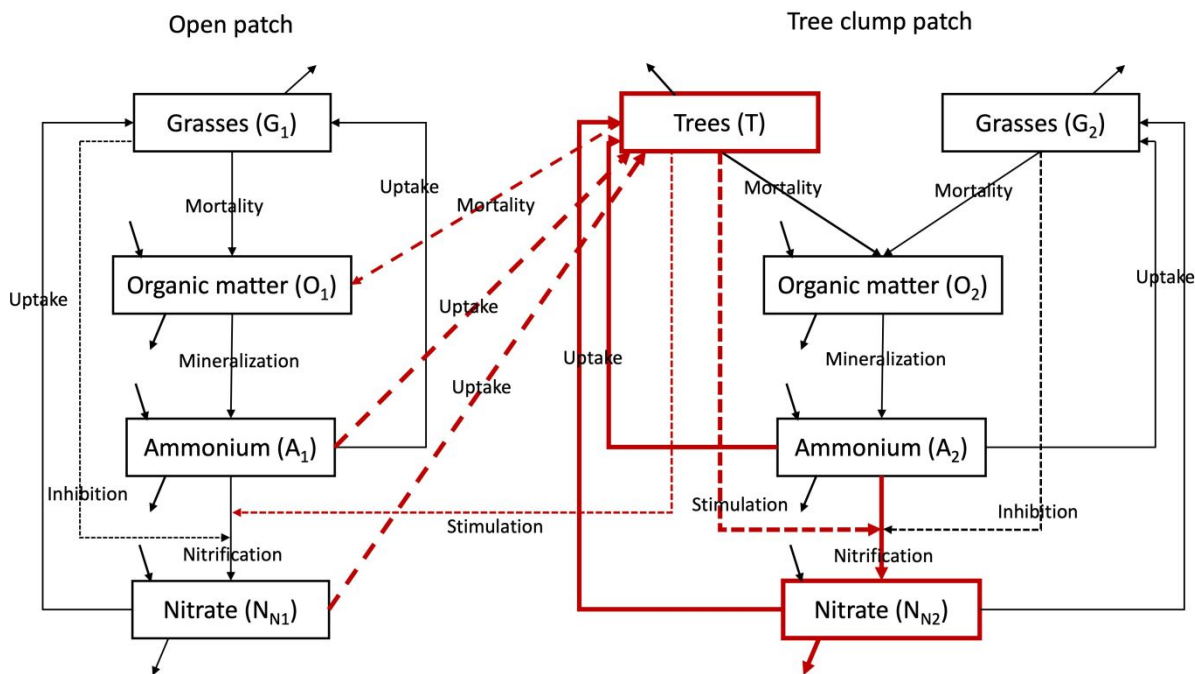
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98 **Appendix S3: Graphical representation of scenarios of invasion by trees versus invasion by**  
 99 **grasses**

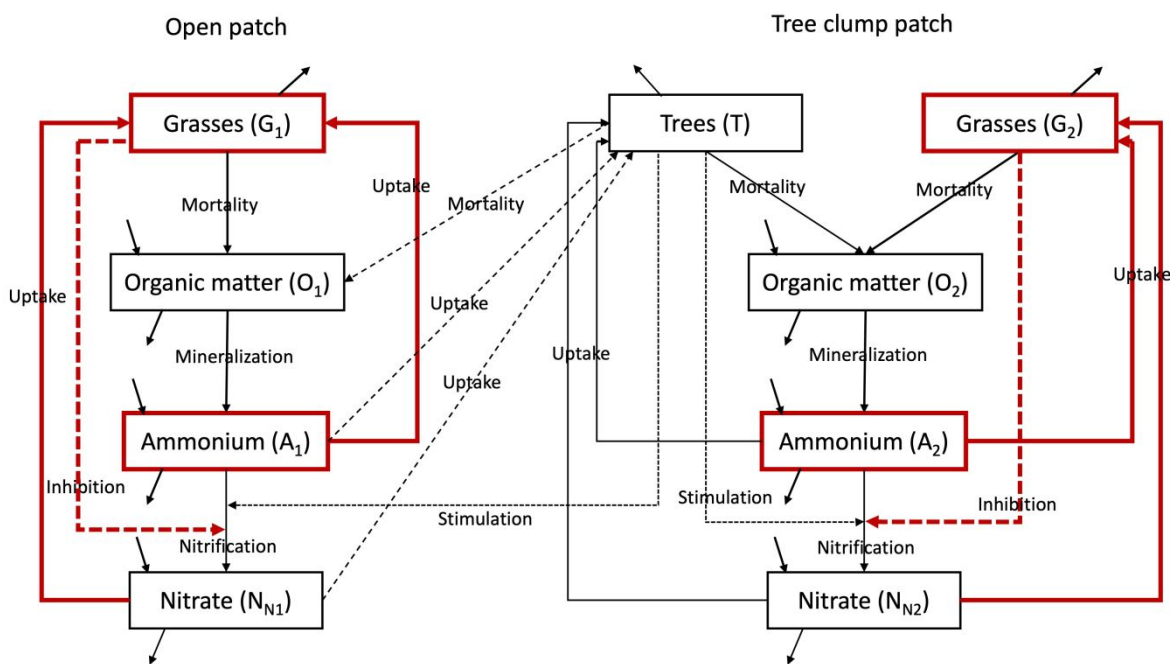
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102 Figure S3-a

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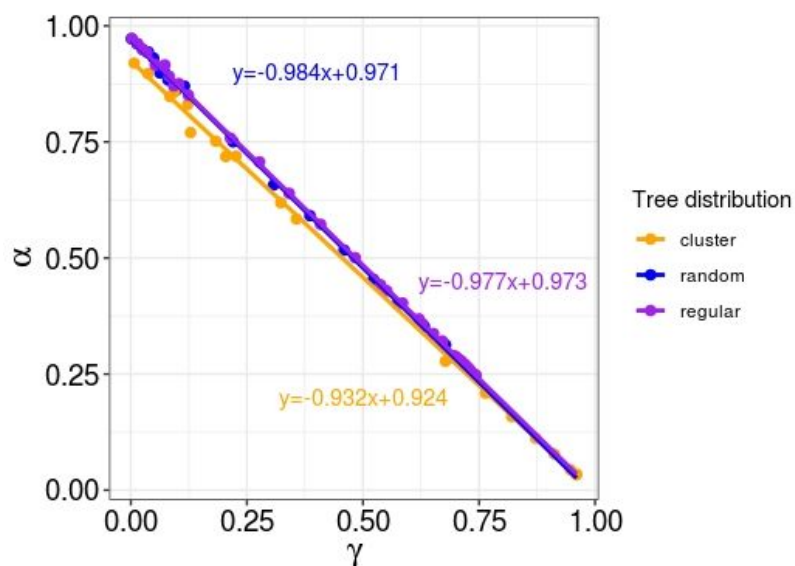
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106 Figure S3-b

#### 107 **Appendix S4: Relation between soil exploration by tree roots and tree cover**

108 We performed simulations for different tree distributions to determine the relation between the  
 109 proportion of tree roots in the open ( $\alpha$ ) and tree cover ( $\gamma$ ) to analyze the effect of spatial patterns on  
 110 tree-grass coexistence. This relation has been tested for random, cluster and regular tree distributions.  
 111 We considered trees with 2 m crown radius and 12 m root radius for each distribution in 1ha plot.  
 112 For all spatial distributions tested, a negative linear relation was observed between  $\alpha$  and  $\gamma$  (p-value  
 113  $< 0.0001$  and  $R^2=0.998$  for random; p-value  $< 0.0001$  and  $R^2=0.999$  for cluster; p-value  $< 0.0001$  and  
 114  $R^2=0.999$  for regular tree pattern).  $\alpha$  significantly decreases while  $\gamma$  increases regardless tree  
 115 distributions. In contrast to the results of the main text where cluster distribution was different to  
 116 random and regular distributions (Figure 1a), we observe here that the relation between  $\alpha$  and  $\gamma$  is  
 117 virtually the same for all patterns. This leads to these linear equations:  $\alpha = -0.984\gamma + 0.971$ ,  $\alpha = -0.977\gamma$   
 118  $+ 0.973$  and  $\alpha = -0.932\gamma + 0.924$  respectively for random, regular and clustered tree distributions.



130 Figure S4

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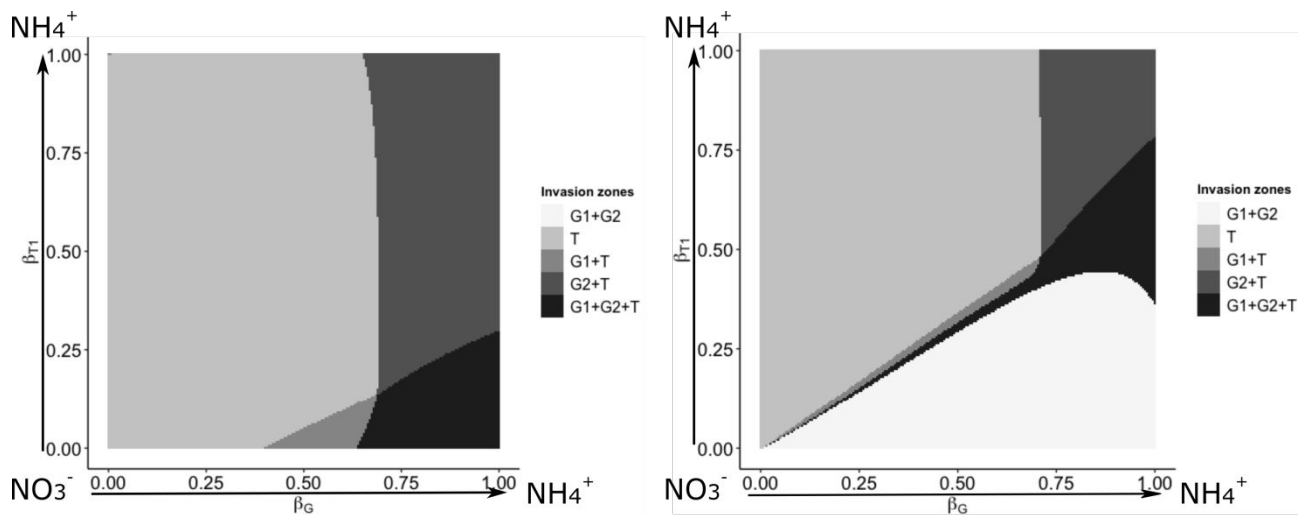
134 **Appendix S5: Regular distribution**135  
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Figure S5-a

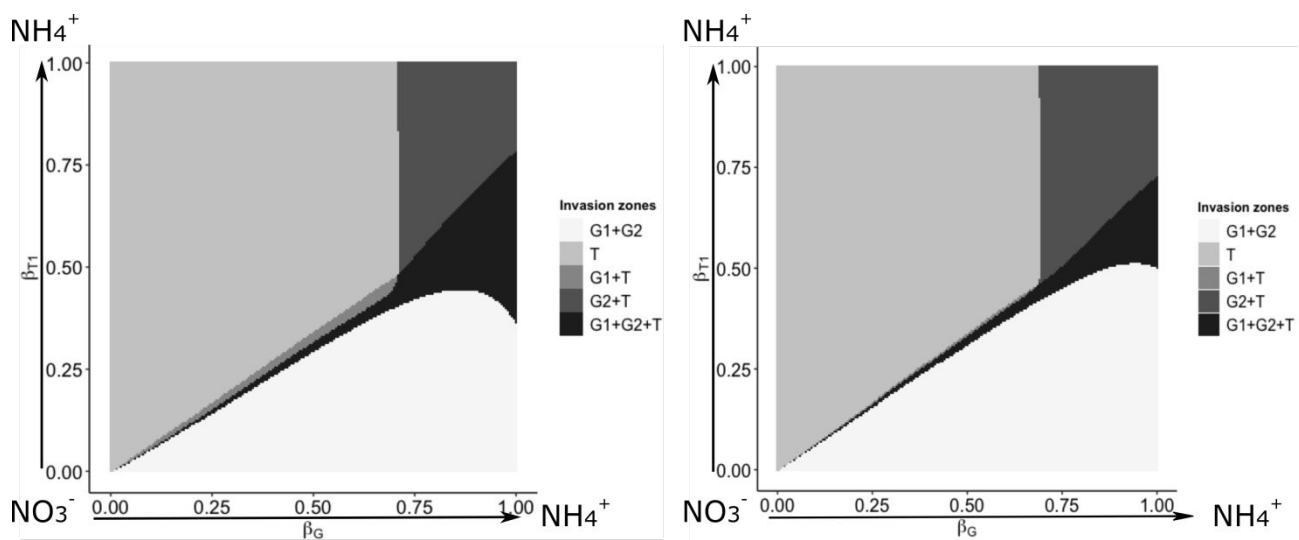
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Figure S5-b

156 **Appendix S6: Effect of tree preference under their canopy depending on spatial tree**  
157 **distributions**

158 We did simulations for different combinations of grass and tree preference for  $\text{NH}_4^+$  in the open.  
159 Here, we tested different tree preference for  $\text{NH}_4^+$  under tree canopy by gradually increasing tree  
160 preference for  $\text{NH}_4^+$  under their canopy ( $\beta_{T2} = 0.35$ ;  $\beta_{T2} = 0.5$ ) knowing that the value by default used  
161 in the main text is  $\beta_{T2} = 0.25$ . Regarding random pattern, when tree preference under tree canopy for  
162  $\text{NH}_4^+$  increases ( $\beta_{T2} = 0.35$ ), trees tend to exclude grasses, which reduces the zone of savanna. This  
163 also increases conditions of coexistence between trees and grasses in the open. When tree preference  
164 under tree canopy for  $\text{NH}_4^+$  increases further ( $\beta_{T2} = 0.5$ ), the zone of savanna becomes very small  
165 while the zone of tree-grass mosaic increases. The overall pattern is similar for cluster pattern but the  
166 region of coexistence between trees and grasses in the open is much larger than in the random tree  
167 pattern case.

168 Increasing tree preference for  $\text{NH}_4^+$  under tree canopy favors the establishment of trees and the  
169 exclusion of grasses in random and cluster patterns. This also leads to an increase of the zone of tree-  
170 grass mosaic (trees and grasses in the open) but strongly reduces the zone of savanna (grasses grow  
171 both under tree canopy and in the open) in both tree patterns.

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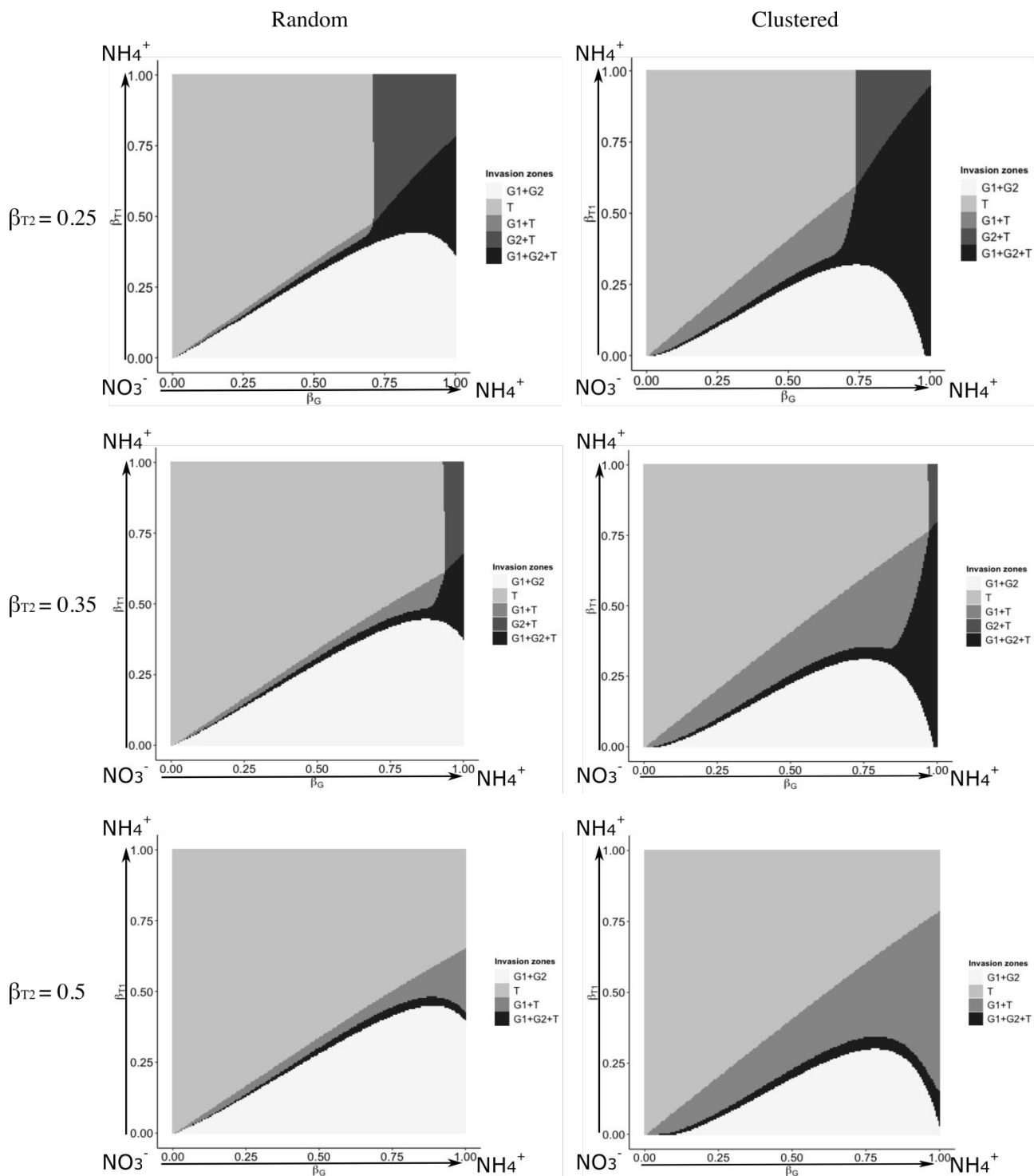
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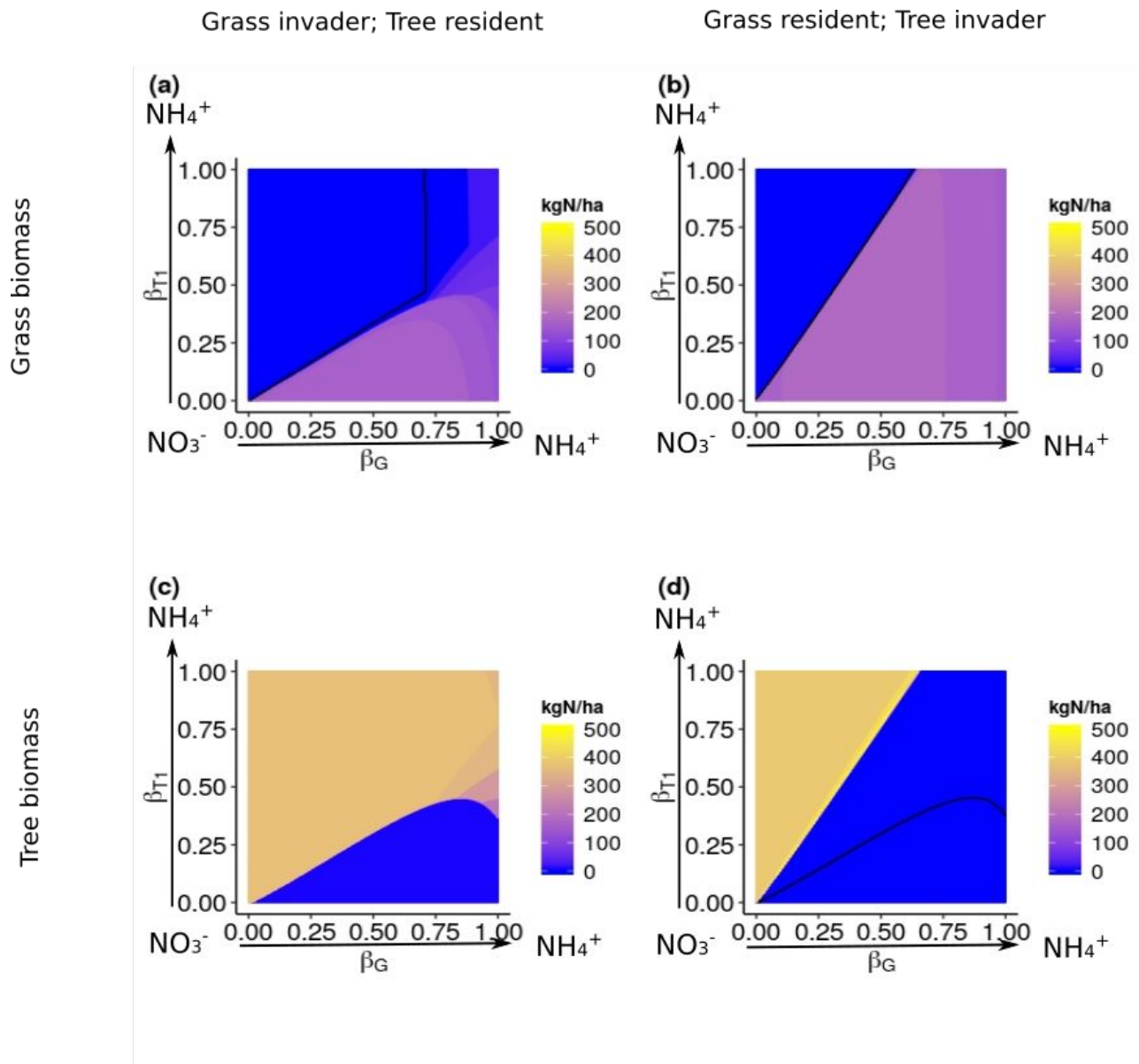
188 Figure S6

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191 **Appendix S7: Plant biomass depending on tree distributions**

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194 Figure S7-a

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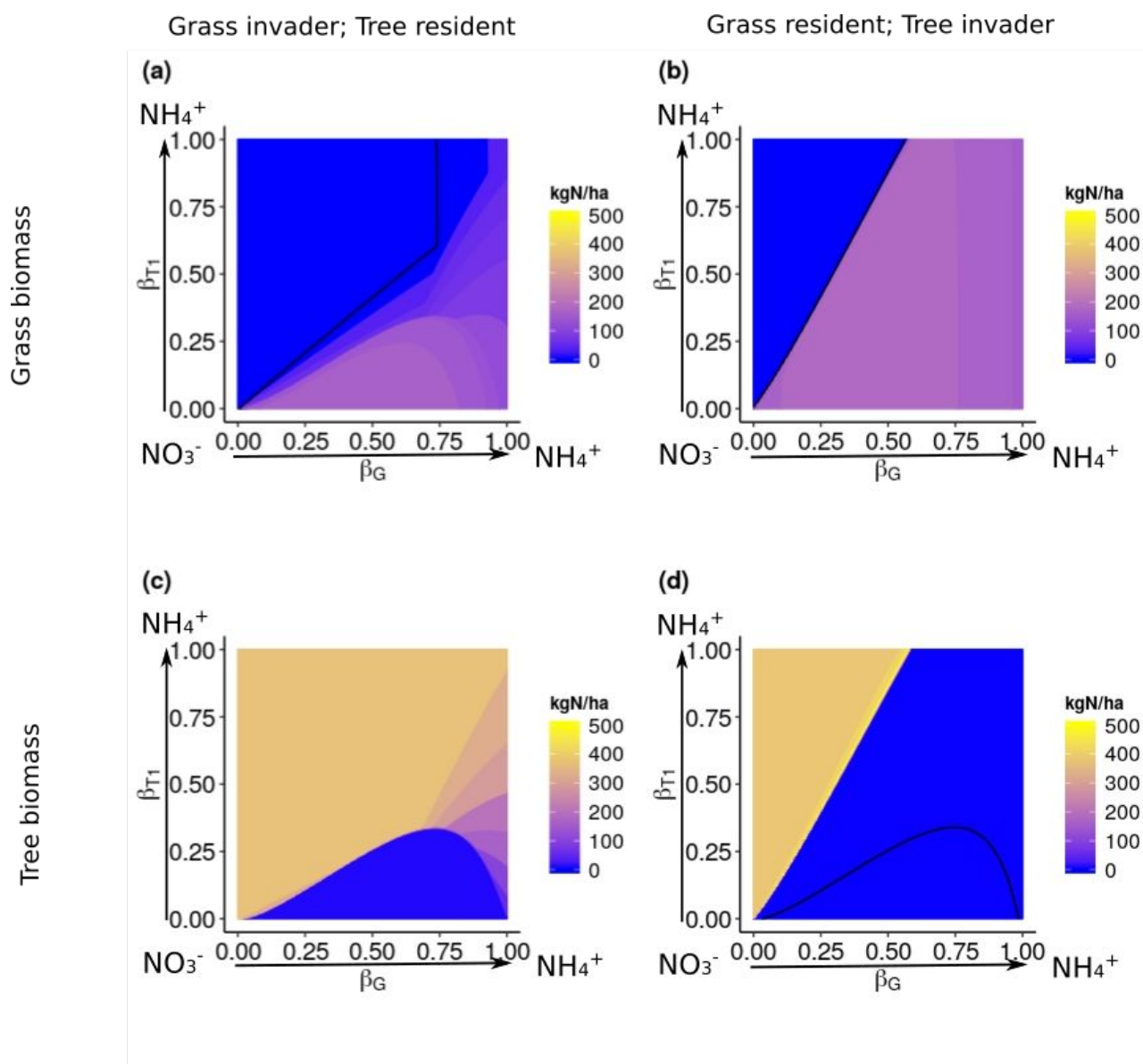
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205 Figure S7-b

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