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RESEARCH ARTICLE

Spatial heterogeneity of nitrification contributes to tree–grass coexistence in West African savannas

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Abstract

1. In savannas, the coexistence between trees and grasses is determined by complex mechanisms based on water partitioning and disturbances. But little is known about the contribution of other resources, such as soil nitrogen (N). In West African savannas, nitrification inhibition by grasses and nitrification stimulation by trees create spatial heterogeneity in nitrification fluxes and N stocks. Savanna trees can also extend part of their roots in the surrounding open area to absorb N.
2. To investigate the role of the spatial heterogeneity of nitrification in tree–grass coexistence, we used a two-patch model that simulates N dynamics between an open patch (without trees) and a tree clump patch (trees with grasses under their canopy). The open patch was characterized by a low nitrification rate, while the tree clump patch was characterized by a high nitrification rate. Both patches were connected through horizontal fluxes due to soil horizontal exploration by tree roots. We tested coexistence for different spatial tree distributions, as they are known to strongly influence savanna dynamics.
3. Our results show that the spatial heterogeneity of nitrification induces spatial partitioning between ammonium (NH_4^+) and nitrate (NO_3^-) promoting tree–grass coexistence. As nitrification inhibition by grasses leads to high NH_4^+ availability in the open, the possibilities of coexistence are optimized when trees have different preferences in the open versus under their canopy. Thus, tree–grass coexistence is observed when grasses prefer NH_4^+, while trees prefer NH_4^+ in the open and NO_3^- under their canopy.
4. Contrary to random tree distribution, tree clumping enhances tree–grass coexistence. Intraspecific aggregation strengthens the effect of spatial heterogeneity, which decreases interspecific competition and favours tree–grass coexistence. On the contrary, increasing the surface explored by tree roots in the open tends to increase tree–grass competition. This enhances the competitive ability of trees for N acquisition and consequently favours tree invasion.
5. *Synthesis*. This study shows that this new coexistence mechanism based on mineral N partitioning into NH_4^+ and NO_3^- can be determinant in the functioning of

West African humid savannas. This mechanism likely interacts with mechanisms based on disturbances, but such interactions should be studied using new models.

KEYWORDS
nitrification, nitrogen partitioning, preference for NH_4^+ versus NO_3^-, savanna, spatial heterogeneity, spatial tree distribution, tree–grass coexistence

1 | INTRODUCTION

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

In West African savannas, the dominant perennial grass species inhibit nitrification, nitrification being the process of transformation of ammonium (NH_4^+) into nitrate (NO_3^-) (Lata et al., 2004; Srikanthasamy et al., 2018; Subbarao et al., 2009). This biological nitrification inhibition (BNI) occurs through the release of grass root exudates impeding the activity of nitrifying microorganisms (Lata et al., 2004; Srikanthasamy et al., 2018). Because NH_4^+ is less prone to leaching than NO_3^-, keeping nitrogen (N) in the NH_4^+ form decreases N losses by NO_3^- leaching and therefore maintains a high primary productivity (Boudsocq et al., 2009). On the contrary, in the Lamto humid savanna (Côte d'Ivoire), the dominant tree species have been found to stimulate nitrification (Srikanthasamy et al., 2018). The mechanism explaining this stimulation is not known, but one hypothesis would be that as for grasses, specific molecules from the tree root system directly impact microbial communities. Another hypothesis is that the observed increase in soil organic matter and soil humidity below the tree canopy could also increase the activity of soil microorganisms and therefore mineralization and nitrification processes (Mordelet et al., 1993; Srikanthasamy et al., 2018).

In nutrient-limited ecosystems such as savannas, plant–soil feedbacks on N cycling can locally alter N availability (Knops et al., 2002) by creating a spatial heterogeneity in soil resources, and thereby, influencing primary productivity. Trees and grasses, through their respective stimulation and inhibition strategies, could induce resource partitioning, if grasses preferentially absorb NH_4^+ and trees NO_3^-, promoting tree–grass coexistence in the Lamto savanna (Boudsocq et al., 2012; Konaré et al., 2019). Some studies have shown that plant preferences for different chemical N forms (organic and mineral N) can facilitate their coexistence (Ashton et al., 2010; McKane et al., 2002). The spatial heterogeneity due to nitrification heterogeneity could further reduce niche overlap, likely decreasing interspecific interactions and promoting coexistence of different species even on a single limiting resource (Barot & Gignoux, 2004; Chesson, 2000; Huston & DeAngelis, 1994). This leads to a complex picture that requires a spatially structured model to understand the consequences of plant–soil feedbacks on the availability of NH_4^+ and NO_3^- and tree–grass coexistence.

Many studies highlighted the relevance of spatial patterns in ecological dynamics (Grimm et al., 1996; Grimm & Railsback, 2012). For example, intraspecific aggregation decreases the strength of interspecific competition (Pacala, 1997; Stoll & Prati, 2001), which can slow down competitive exclusion (Armstrong & McGehee, 1980). The spatial tree distribution is known to play an important role in savanna dynamics and is strongly affected by disturbances (Menaut et al., 1990). Furthermore, tree clumps are generally considered as nutrient-rich patches (Mordelet et al., 1993) and this higher soil fertility under the tree canopy is partly due to the horizontal soil exploration by tree roots in the open, as it improves nutrient transfers between the open and tree clumps (Konaré et al., 2021). Although spatial heterogeneity tends to foster niche partitioning (Amarasekare, 2003), horizontal fluxes can minimize the impact of this heterogeneity by homogenizing the availability of NH_4^+ and NO_3^- between the two patches (Barot et al., 2014, 2015). Therefore, this could be influential for predictions of tree–grass coexistence.

In contrast to the work of Konaré et al. (2019) that does not consider spatial heterogeneity (all plants explore the same N pools) and Konaré et al. (2021) that focused on the effects of the spatial heterogeneity of nitrification fluxes on N fluxes and N budget, the goal of this study is to analyse the role of spatial heterogeneity in tree–grass coexistence. To do so, we used a modified version of the previously published two-patch model (Konaré et al., 2021) considering an open area patch with a low nitrification rate and a tree clump patch with a high nitrification rate. These two patches are interconnected by horizontal fluxes (due to horizontal exploration of the soil in the open area by tree roots). The novelty of this model relies on considering the relation between two model parameters (the proportion of tree roots in the open and the proportion of the savanna surface covered by tree clumps) that depends on spatial tree distribution. Using this general model, we tested the following hypotheses: (i) Compared to the mean-field model (Konaré et al., 2019), accounting for the existence of distinct N pools below and outside tree clumps fosters coexistence. (ii) Spatial heterogeneity in nitrification increases the likelihood of tree–grass coexistence with grasses preferring NH_4^+ and trees preferring NO_3^- under tree canopy and NH_4^+ in the open. Indeed, this spatial heterogeneity leads to a spatial niche partitioning that reduces exclusion and favours coexistence. (iii) Tree–grass coexistence depends on the spatial distribution of trees and is facilitated when trees are clumped. More specifically, tree clumping reduces soil exploration by tree roots in the open and thus reduces competition between trees and grasses in the open. (iv) Increasing the surface explored by tree roots in the open increases horizontal fluxes between the open and the tree clump patches, which increases the competition between trees and grasses for N and consequently reduces the chances of coexistence.

2 | MATERIALS AND METHODS

2.1 | Description of the two-patch model

The two-patch model explores competitive interactions between trees and grasses through two patches: an open patch occupied by grasses and some tree roots (patch 1), and a tree clump patch occupied by trees with grasses growing below their canopy (patch 2) (Appendix S1). This model is a spatially explicit extension of a previously published mean-field model (Konaré et al., 2019). The model tracks N dynamics between the plant compartments: grass biomass (G_1) in the open and, grass (G_2) and tree biomass (T) in the tree clump patch, and the soil compartments: soil organic matter (O), ammonium (N_A) and nitrate (N_N) in both patches (see Figure 1; Konaré et al., 2021). Spatial heterogeneity due to nitrification inhibition (BNI) by grasses and nitrification stimulation by trees is represented by a low nitrification rate in the open (n_1) and a high nitrification rate under tree clumps (n_2). Both patches are interconnected through horizontal fluxes due to the ability of trees to extend horizontally their roots to take up nutrients in the open. In the model, N is supposed to be the limiting factor in primary production, and the growth of grasses and trees depends on the acquisition of mineral N forms, that can be acquired in two forms (NH_4^+ and NO_3^-) with a certain preference (β) for NH_4^+ versus NO_3^-. This preference ranges between 0 and 1 with high values of β corresponding to a high preference for NH_4^+. N is absorbed by plants through N uptake rates $\beta\, u$ for NH_4^+ uptake and $(1-\beta)\, u$ for NO_3^- uptake. Plants release N into an organic N pool at constant mortality rates d_G, d_l and d_r respectively for grasses, tree leaves and tree roots. Organic N is mineralized into NH_4^+ at a rate m and NH_4^+ can be transformed into NO_3^- at a rate n. Each patch receives N inputs through dry and wet depositions that provide N under organic and mineral forms into O, N_A and N_N compartments, respectively, at rates i_O, i_{NA} and i_{NN}. Nonsymbiotic fixation contributes to the input of NH_4^+ and is included in i_{NA} (Abbadie, 2006). N losses in savannas result from the burning of the plant compartments (l_G and l_T), and leaching for other compartments (l_O, l_{NA} and l_{NN}). NO_3^- losses by denitrification are included in l_{NN}. All parameters but nitrification rates are equal between the two patches to keep the model relatively simple and focus on the

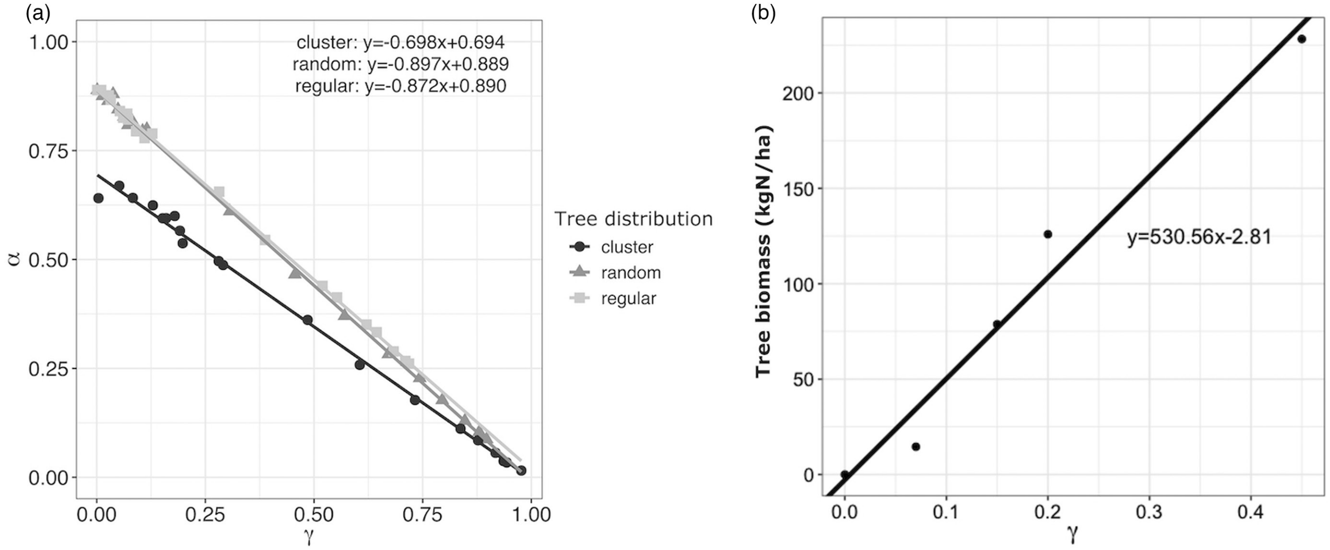

FIGURE 1 (a) Proportion of tree roots in the open (α) as a function of tree cover (γ) according to cluster, random and regular tree distribution for a root radius equals to 6 m. (b) Tree biomass as a function of tree cover (γ). Panel a represents results of simulations obtained by generating different spatial point patterns (random, clustered and regular: see Section 2). In panel (b), we used data from Menaut and César (1979).

effects of nitrification heterogeneity (see model parameter Table, Appendix S2). All compartments are N stocks expressed as a quantity of N by surface unit, that is, kilograms of N per hectare of savanna (kg N/ha). The system of differential equations is the same as used in Konaré et al. (2021):

Open patch (patch 1)

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

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

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

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

Tree clump patch (patch 2)

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

$$\begin{aligned}\frac{dT}{dt} &= \gamma\,(1-\alpha)\left(\beta_{T2}\, u_r\, N_{A2}\, r\, T + \left(1-\beta_{T2}\right) u_r\, N_{N2}\, r\, T\right)\\ &+ \alpha\left(\beta_{T1}\, u_r N_{A1}\, r\, T + \left(1-\beta_{T1}\right) u_r\, N_{N1}\, r\, T\right) \quad (6)\\ &- \left(d_l\,(1-r) + d_r \alpha\, r + (1-\alpha)\, d_r\, r + l_T\right) T,\end{aligned}$$

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

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

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

2.2 | Spatial setting of the model

The description of the spatial setting in the model is based on the proportion of tree roots in the open (α) and the proportion of the surface of the savanna covered by tree clumps (γ) (leaving ($1-\gamma$) to the open savanna). Compared to Konaré et al. (2021) in which α and γ had fixed values, in this version of the model, α is a function of γ and γ is a function of tree biomass (T). We assume that α depends on the proportion of tree cover and the spatial patterns of trees: for a given canopy and root system radius, α should decrease with γ. However, this relationship should also depend on tree distribution with lower values of α when trees are clumped and high values of α when they are randomly or regularly distributed. Although tree distribution can vary in different savanna ecosystems, it is often clustered (Barot et al., 1999; Gignoux et al., 2006). Similarly, we assume a positive relationship between γ and tree biomass T: the more trees, the more surface they occupy in the savanna.

The shape of the relation between α and γ was studied by simulating different distributions of trees (random, clustered and regular). We assumed that trees were represented as two superimposed discs describing the canopy and the root system since the majority of tree roots have been found within a radius 10 m away from tree clump centre (Jean-Claude Menaut, personal communication). In our simulations, the canopy radius was set to 2 m and the root system radius to 6 m. The relationship between α and γ was obtained by calculating the proportion of the root system that did not fall under the canopy of other trees for each tree distribution and for different tree densities exploring a wide range of tree cover. We calculated the relation between α and γ for random, clumped and regular tree distributions. To simulate random patterns, a Poisson process with a tree density varying from 1 to 100 trees ha^{-1} by step of 10 and from 100 to 2000 trees ha^{-1} by step of 200 was used. Clumped patterns were obtained using a Matérn cluster process (Matérn, 1960) with a tree density varying from 1 to 100 trees ha^{-1} by step of 10 and from 100 to 1000 trees ha^{-1} by step of 100 with a mean clump radius of 2 m and a mean number of trees per clump of 10. Finally, regular patterns were modelled using a Matérn hard-core process (Matérn, 1960, 1986) with an inhibition distance of 2 m and the same tree densities as the random patterns. To determine the relation between α and γ, and between γ and T, we calculated the proportion of tree roots outside the tree canopy at the individual scale and the mean of all individual values to obtain α for a given tree density. We then calculated γ for each tree density by determining the total space occupied by trees. Linear regression models were then used to determine the relation between α and γ. Additionally, we used data from Menaut and César (1979) to establish the relationship between γ and tree biomass (T) through a linear regression model. The equations from linear models and parameters were included in the two-patch model to link α, γ and T.

2.3 | Model analysis and parameterization

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

We used the same parameter sets as in Konaré et al. (2021; see appendix S2) but run a completely different simulation experiment.

These parameters are based on data from the Lamto savanna in Côte d'Ivoire (06°13′ N, 05°02′ W) (Abbadie et al., 2006) (Appendix S2).

Tree–grass coexistence was determined using the mutual invasibility criterion (Chesson & Ellner, 1989). This criterion considers a pair of invader and resident species (e.g. grasses invading a forest, starting with a negligible biomass of 0.01 kg N/ha compared to the tree biomass, with a high biomass of 10 kg N/ha, and then the reverse situation with trees invading a grassland). When the two species are able to invade each other, they are assumed to mutually coexist over the long term (Chesson & Ellner, 1989). Nitrification stimulation under tree clumps suggests a preference of trees for NO_3^- at least for roots under the tree canopy. Because NH_4^+ should be the dominant N form in the open due to nitrification inhibition by grasses, a preference of trees for NH_4^+ in the open is more expected. Therefore, we decided to distinguish the preference of trees for NH_4^+ versus NO_3^- in the open patch (β_{T1}) and under tree clumps (β_{T2}) and the preference of trees in the tree clump patch was fixed to a constant value ($\beta_{T2}=0.25$). Simulations of N stocks and fluxes were performed for different combinations of grass and tree preference for NH_4^+ versus NO_3^- in the open (β_G and β_{T1}) varying between 0 and 1 with an increment of 0.005. We first simulated mutual invasion between trees and grasses for different combinations of grass and tree preference for NH_4^+ versus NO_3^- (tree preference was the same in the open and under tree canopy: β_T) versus different combinations of grass and tree preferences for NH_4^+ versus NO_3^- in the open (β_{T1}) to compare the effect of tree preference on tree–grass coexistence. Nitrification rates in the open and under tree clumps were calculated by dividing nitrification fluxes under grasses and under trees by their respective ammonium stocks (Srikanthasamy et al., 2018). We increased the nitrification rate in the open to compare a spatial homogeneity to a spatial heterogeneous nitrification rate to test the importance of heterogeneity in nitrification flux on tree–grass coexistence. Moreover, because the proportion of tree roots in the open does not depend only on tree density or biomass, but also on the spatial distribution of individual trees, we tested the effects of tree distributions in space (random, regular and clustered) on tree–grass coexistence. We tested the sensitivity of the results to the root radius by increasing this radius from 6 to 12 m to assess the relationship between α and γ and then analyse the effect of these new equations on the coexistence between trees and grasses.

3 | RESULTS

3.1 | Links between soil exploration by tree roots and tree cover and between tree biomass and tree cover

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

3.2 | Tree–grass coexistence is affected by the preference of trees for NH_4^+ in the open versus under the tree canopy

The simulation of the model for the clustered tree distribution leads to three cases of coexistence: (1) a case where trees and grasses are spatially separated (no grasses under trees, only in the open hereafter called tree–grass mosaic), (2) a case where grasses can only grow under tree clumps (no open area) hereafter called savanna woodland and (3) a case where grasses grow both under tree canopy and in the open (hereafter called savanna). When the preference of trees is the same in the open and under the tree canopy (Figure 2a), grasses successfully invade and exclude trees for a wide range of grass preferences for NH_4^+ versus NO_3^- and when trees prefer NO_3^-. Tree–grass mosaic occurs when grasses have a higher preference for NH_4^+ than trees ($0 < \beta_T < 0.8$). On the contrary, when tree preference for NH_4^+ is higher than for grasses, trees completely invade and exclude grasses. We also observe a small portion of the parameter space where tree clumps are established when grasses prefer NO_3^- and trees strongly prefer NH_4^+ ($\beta_T > 0.98$). Savanna tree–grass coexistence is possible when grasses have a high preference for NH_4^+ and trees prefer NO_3^- and when grasses have a higher preference for NH_4^+ than trees ($0 < \beta_T < 0.3$).

If trees have different preferences in the open (β_{T1} ranged between 0 and 1) versus under the tree canopy (β_{T2} constant) (Figure 2b), the sizes of the zone of savanna woodland and savanna strongly increase while the zone of tree–grass mosaic decreases. Savanna is favoured for a wide range of tree preferences in the open (β_{T1}) and a grass preference for NH_4^+. The establishment of tree clumps becomes possible when grasses and trees in the open prefer NH_4^+. Taken together, a same tree preference in the open and under tree canopy reduces possibilities of complete coexistence between trees and grasses but favours tree–grass mosaic, while different tree preference in the open and under tree canopy increases possibilities of coexistence between trees and, grasses in the open and under tree canopy. Thus, we consider different tree preference in the open versus under tree canopy for all other simulations.

3.3 | Tree–grass coexistence depends on the spatial tree distribution

Because the results of the regular and random tree distributions are virtually the same (Appendix S5), we only presented clustered and random distributions in the main text. Tree distribution strongly influences the conditions of coexistence between trees and grasses (Figure 3). For random tree distribution, grasses invade and exclude trees when grasses have a higher preference for NH_4^+ than trees in the open ($\beta_{T1} < 0.4$). However, when tree roots in the open have a higher preference for NH_4^+ than grasses ($\beta_G < 0.7$), trees successfully invade and exclude grasses. The model also predicts a zone in which savanna establishes when $\beta_G > 0.7$ and $0.4 < \beta_{T1} < 0.73$, a zone in which tree clumps invade when grasses and trees in the open prefer NH_4^+ and a small zone of tree–grass mosaic.

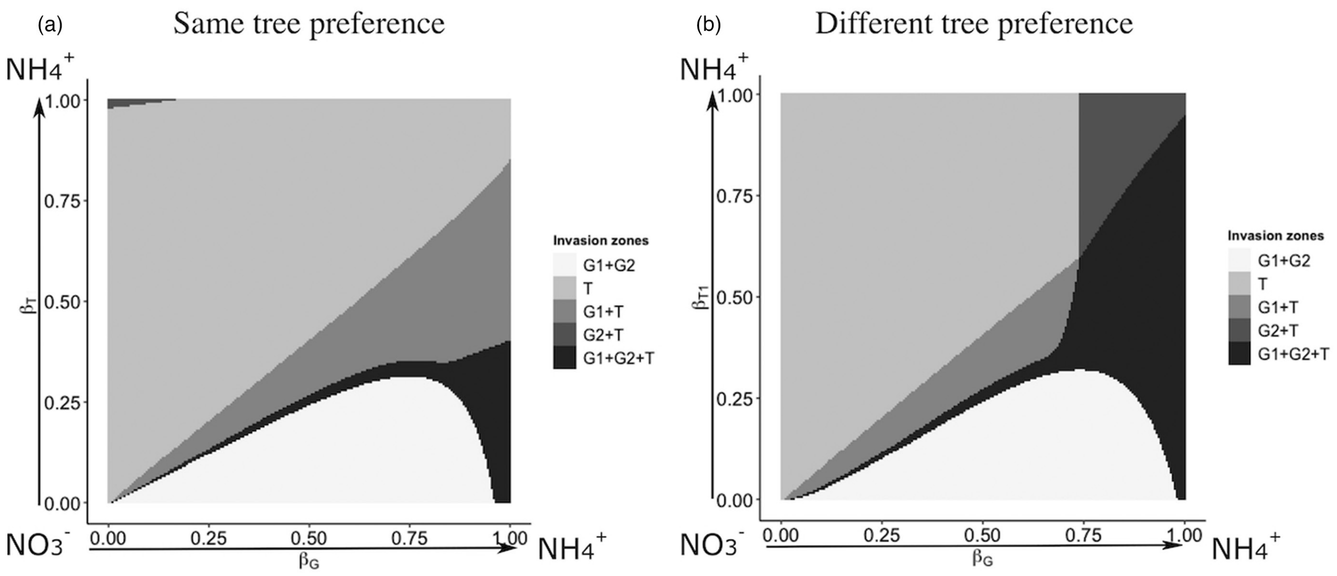

FIGURE 2 Mutual invasibility plots between trees and grasses according to grass (β_G) and tree preference for NH_4^+. (a) Trees have identical preferences for NH_4^+ in the open and the tree patches (β_T). (b) Trees have different preferences for NH_4^+ in the open (β_T) and the tree patch (β_{T2}). In these simulations, β_{T2} was set constant to 0.25. Simulations correspond to clustered tree distributions. Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree–grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

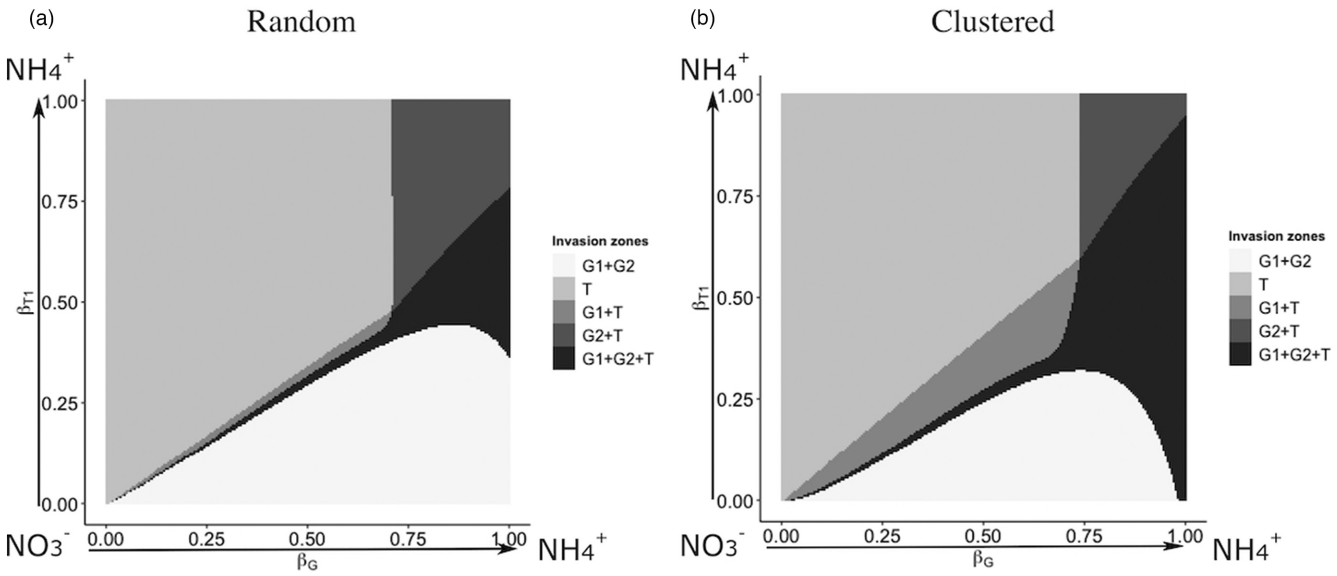

FIGURE 3 Mutual invasibility plots between trees and grasses according to random (a) and clustered (b) tree distributions at the savanna scale. Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree–grass mosaic (coexistence between trees and grasses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

Compared to random tree distribution, the clustered pattern strongly increases the size of the zones of savanna and tree–grass mosaic. Tree–grass mosaic is enhanced when the grass preference for NH_4^+ is higher than the tree preference for NH_4^+ in the open (β_{T1}). The savanna zone extends to a wide range of β_{T1} values and a preference of grasses for NH_4^+. Switching from random to clustered tree distribution also reduces the size of the zone of invasion by grasses, trees or savanna woodland (Appendix S3).

3.4 | Comparison between the cases of spatial heterogeneity and spatial homogeneity

The spatial heterogeneity of nitrification due to its control by plants alters conditions of coexistence between trees and grasses. We compared the case of spatial heterogeneity (Figure 3) with a case of spatial homogeneity where grasses do not inhibit nitrification (Figure 4). In the case of a random tree distribution, increasing the nitrification rate in the open promotes invasion by tree clumps ($\beta_G > 0.69$ and $\beta_{T1} > 0.35$) or by trees only ($\beta_G < 0.69$ and for all combinations of β_{T1}). Compared to cases where nitrification is spatially heterogeneous (Figure 3), we observed tree–grass mosaic zone for $0.4 < \beta_G < 0.62$ and $\beta_{T1} < 0.13$ and a savanna zone when grasses prefer NH_4^+ ($\beta_G > 0.62$) and trees prefer NO_3^- in the open ($\beta_{T1} < 0.28$) in the spatial homogeneity case. For a clustered tree distribution, the overall pattern is virtually the same, but a second zone of tree–grass mosaic appears when grasses and trees in the open strongly prefer, respectively, NO_3^- ($\beta_G < 0.2$) and NH_4^+ ($\beta_{T1} > 0.95$). Increasing the nitrification rate reduces the total coexistence between trees and grasses and facilitates zones with only trees or trees with grasses under their canopy. This shows that different nitrification rates in the open and in the tree clump patch improve the chances of tree–grass coexistence.

3.5 | Soil exploration by tree roots affects tree–grass coexistence

Figure 5 shows the outcome of mutual invasion between trees and grasses when the radius of the tree root system is increased from 6 to 12 m. As described above, savanna (grasses grow under tree canopy and in the open) occurs in cases of random distribution when $\beta_G > 0.7$ and $0.4 < \beta_{T1} < 0.73$ and the size of this zone increases and extends to more combinations of β_{T1} when we switch from a random tree distribution to a clustered tree distribution (root radius = 6 m; Figure 5a,b). We observe the same tendencies when the root radius is increased to 12 m (Appendix S4). Overall, clustered distributions tend to increase the size of the savanna zone. However, increasing the surface explored by tree roots reduces the sizes of the zone of tree–grass coexistence in cases of both random and clustered distributions (Figure 5c,d). This is more perceptible for clustered patterns for which the size of the savanna and tree–grass mosaic zones largely decreases while the zone of invasion by grasses increases (Figure 5d).

4 | DISCUSSION

In our model, tree–grass coexistence occurs when plants have contrasted preferences for NH_4^+ versus NO_3^-. This is in agreement with theories showing that the coexistence of different species is possible when they differ in their use of resources (Armstrong & McGehee, 1980). This is also in agreement with published works on competition for NH_4^+ and

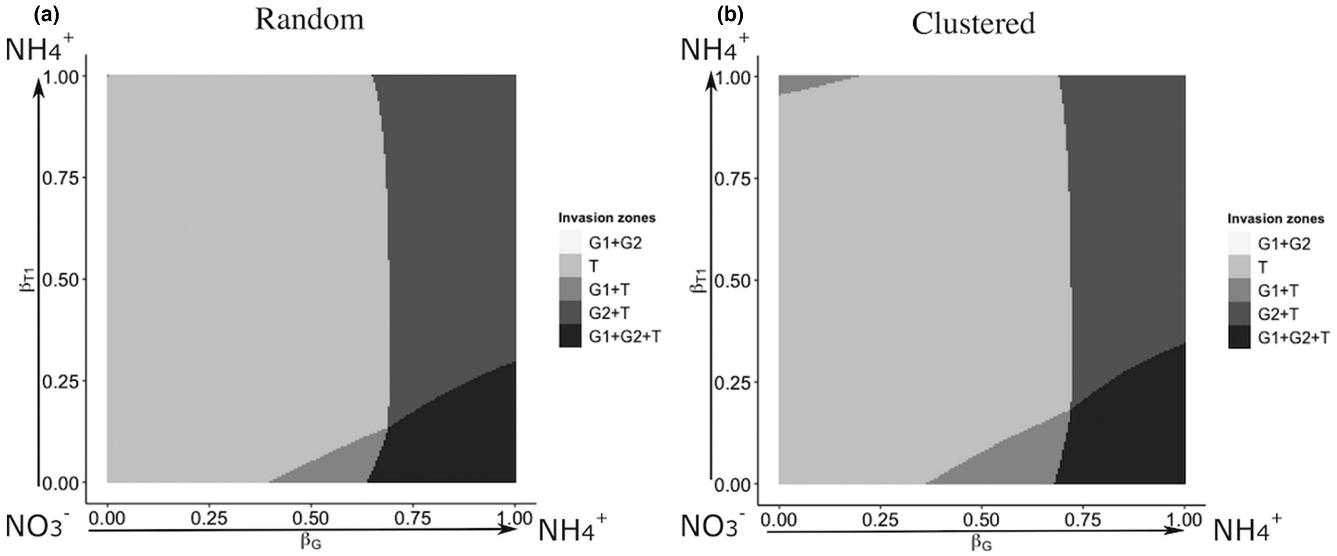

FIGURE 4 Mutual invasibility plots between trees and grasses according to random (a) and clustered (b) tree distributions at the savanna scale. These figures correspond to cases where grasses do not inhibit nitrification (spatial homogeneity: $n_1 = n_2 = 4.16\ \text{year}^{-1}$). Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree–grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

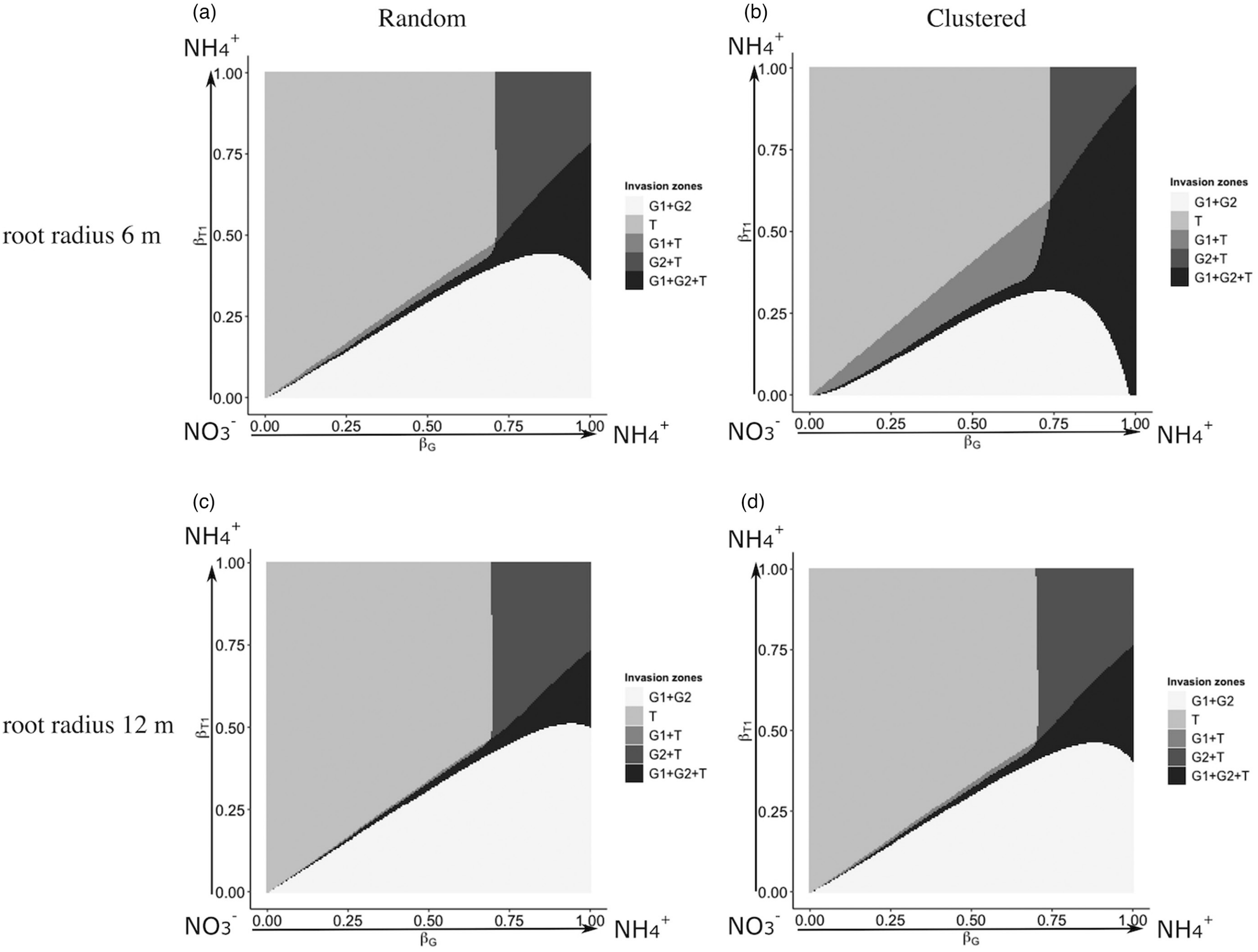

FIGURE 5 Mutual invasibility plots between trees and grasses according to random (a and c) and clustered (b and d) tree distributions at the savanna scale. The first (a and b) and second (c and d) rows of graphs respectively corresponds to simulations of tree distributions with a root system radius of 6 and 12 m when determining the relation between α and γ. Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree–grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

NO_3^- between plants (Boudsocq et al., 2012; Konaré et al., 2019). These results are also supported by empirical studies on N partitioning indicating that plants having different preferences for different chemical N forms can coexist (Ashton et al., 2010; McKane et al., 2002). Mineral N partitioning appears as a stabilizing mechanism (Barot & Gignoux, 2004; Chesson, 2000) that fosters coexistence between savanna trees and grasses. Here, we further analyse the influences of these processes on tree–grass coexistence testing for the effects of spatial heterogeneity in nitrification fluxes (hypothesis 1), mineral N partitioning into NH_4^+ and NO_3^- (hypothesis 2), spatial tree patterns (hypothesis 3) and horizontal soil exploration by tree roots (hypothesis 4).

4.1 | Comparison between the one-patch and the two-patch model

Compared to the mean-field model (Konaré et al., 2019), the two-patch model allows to simulate distinct pools of mineral N available below tree clumps and in the open. Although the sizes of the savanna zone in the two-patch model (cluster distribution; Figure 3) and in the mean-field model (Figure 2a; Konaré et al. (2019)) are not significantly different, the two-patch model predicts different possible cases of coexistence that correspond to different landscape structures. Indeed, while the mean-field model only allows one possible case of tree–grass coexistence, the two-patch model can lead to three types of coexistence: savanna woodland (trees with grasses under their canopy only), tree–grass mosaic (trees with grasses only in the open) or savanna (trees with grasses everywhere). These results are in agreement with theories showing that coexistence in a spatially heterogeneous environment is facilitated (Amarasekare, 2003; Chesson, 2000) even with a single resource. In this case, spatial heterogeneity separates the mineral N resource so that this resource is no longer fully shared between the competitors, leading to more diverse scenarios of coexistence in the two-patch model than in the one-patch model.

4.2 | Heterogeneity in nitrification influences tree–grass coexistence in the Lamto savanna

Studies on resource-based mechanisms of tree–grass coexistence in savannas have focused on water competition (Walker & Noy-Meir, 1982; Walter, 1971). However, little is known about other resources that are essential for plant growth, such as N (Donzelli et al., 2013). In our model, when trees have the same preference in the open and under tree canopy, savannas occur when grasses have a high preference for NH_4^+ and trees a high preference for NO_3^- (Figure 2). This confirms that tree–grass coexistence is possible when grasses prefer NH_4^+ and trees prefer NO_3^- at least under tree canopy. Wang and Macko (2011) studied the preference of grasses according to climatic conditions and found that grasses tend to prefer NH_4^+ in humid areas. Moreover, ongoing studies on *Hyparrhenia diplandra* in the Lamto savanna (Sébastien Barot, personal communication) as well as a study on *Andropogon gayanus* (Rossiter-Rachor et al., 2009) suggest that these two species that inhibit nitrification, have a preference for NH_4^+. Unlike the mean-field model where trees and grasses coexist when grasses prefer NO_3^- and trees prefer NH_4^+ (Konaré et al., 2019), in the two-patch model, tree–grass coexistence becomes possible when grasses prefer NH_4^+ and trees prefer NO_3^-. This is more in agreement with the Lamto savanna case, as grasses are known to inhibit nitrification while trees stimulate it (Lata et al., 2004; Srikanthasamy et al., 2018). The limitation of N in the Lamto savanna (Abbadie et al., 2006) has induced the evolution of different strategies: a conservative strategy for grasses through the BNI capacity and an acquisitive strategy for trees through the stimulation of nitrification (Barot et al., 2015).

Konaré et al. (2021) showed that the uptake of NH_4^+ by tree roots outside the tree canopy (35.58% of total N uptake by trees) increased tree biomass. Our results confirm this scenario because different tree preference for NH_4^+ versus NO_3^- in the open and under tree canopy (trees prefer NH_4^+ in the open and NO_3^- under their canopy) increases the zone of savanna, that is, tree–grass coexistence (Figure 2). Furthermore, simulations testing different values of tree preference for NH_4^+ versus NO_3^- under their canopy showed that increasing tree preference for NH_4^+ under the tree canopy reduces the establishment of savanna zones but promotes tree invasion (Appendix S6). These results suggest that the plasticity of tree root systems in their preference for NH_4^+ versus NO_3^- should occur depending on the spatial distribution of NH_4^+ and NO_3^- (Britto & Kronzucker, 2013). In both cases (same vs. different tree preferences), our results show that local interactions between species and their environment can induce a spatial heterogeneity leading to niche partitioning, and thus promote their coexistence (Amarasekare, 2003; Huston & DeAngelis, 1994). These different impacts of trees and grasses on nitrification create small-scale heterogeneities by increasing the availability of their preferred N form, which induces niche complementarity for N acquisition. In comparison, increasing the nitrification rate in the open reduces coexistence and favours the establishment of zones with only trees and savanna woodlands (Figure 4). Indeed, increasing this rate reduces heterogeneity in nitrification, which increases niche overlap (Amarasekare, 2003; Chesson, 2000) and increases the competitive ability of trees for N. Taken together, these feedbacks based on N recycling tend to stabilize the open and tree clump patches and favour tree–grass coexistence on a larger scale. In addition, the preference for NH_4^+ versus NO_3^- qualitatively influences savanna dynamics, confirming that this preference can have important consequences at the ecosystem scale on vegetation dynamics (Boudsocq et al., 2012) and quantitatively on plant biomass (Appendix S7). While plasticity in plant preference for NH_4^+ versus NO_3^- has already been described, our results suggest that we should acquire experimental results to measure this preference on savanna trees and its spatial variability to analyse the underlying mechanisms along Britto and Kronzucker's arguments (Britto & Kronzucker, 2013).

4.3 | The spatial distribution of trees alters the conditions of coexistence

Many modelling studies have shown that species coexistence could be facilitated by intraspecific clustered distributions (Hartley & Shorrocks, 2002; Inouye, 1999). Our results confirm that coexistence is easier when trees are clumped than when they are randomly distributed. In a random tree distribution, grass and tree roots growing outside tree canopy easily overlap in the open. This increases competitive interactions between trees and grasses for N acquisition in the open through lateral N exchanges following the horizontal soil exploration by tree roots. The strong competition between trees and grasses in the open prevents the establishment of tree–grass mosaic and savanna zones whereas it facilitates invasion by grasses or by trees depending on their preferences for NH_4^+ versus NO_3^-. In contrast, the clumping of trees limits the proportion of tree roots in the open as tree individuals are surrounded by more conspecifics (tree roots tend to be more under the canopy of neighbouring trees). This decreases N transfers between the open and the tree clump patch through horizontal fluxes and highlights the impact of spatialization: intraspecific aggregation tends to foster intraspecific competition over interspecific competition. Some studies found that intraspecific aggregation is influential for species coexistence, as it facilitates the maintenance of weaker competitors (Monzeglio & Stoll, 2005; Stoll & Prati, 2001). Taken together, tree spatial patterns influence the outcomes of competition by impacting the strength of intra- relative to interspecific competition (Stoll & Prati, 2001). In addition, in some savannas (Couteron & Kokou, 1997; Skarpe, 1991) and particularly in the Lamto savanna (Barot et al., 1999; Gignoux et al., 2006), trees often show an aggregated spatial distribution. They form clumps leaving an important proportion of the surface covered by grasses. Tree clumps are maintained by fires: reduced grass biomass under tree shading decreases fire intensity and hence increases tree sapling survival (Gignoux et al., 2006;

Hochberg et al., 1994). This mechanism somehow increases the likelihood of tree–grass coexistence by impeding fires (promoted by grass biomass) to kill all tree saplings. Our results suggest that tree clumps may favour tree–grass coexistence and savanna maintenance through another mechanism: a decrease in the competition for mineral N, but empirical studies are needed to support this effect of tree spatial distribution on savanna dynamics.

4.4 | Impact of horizontal soil exploration on coexistence

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

5 | CONCLUSIONS

Savanna ecosystems can be viewed as small-scale meta-ecosystems (Loreau et al., 2003) where the spatial heterogeneity in nitrification between the two patches and the intensity of lateral N fluxes strongly influence the outcomes of competition between trees and grasses. Our findings confirm that the spatial heterogeneity in nitrification promotes tree–grass coexistence when trees and grasses have different preferences for NH_4^+ versus NO_3^- with grasses preferring NH_4^+ and trees NO_3^- under their canopy. While increasing the soil exploration by tree roots in the open tends to increase the competitive ability of trees to acquire N, intraspecific aggregation through clustered tree distribution intensifies the effect of spatial heterogeneity, which reduces the competition between trees and grasses favouring their coexistence. Mineral N partitioning into NH_4^+ and NO_3^- can play an important role in promoting tree–grass coexistence. Although the ability to inhibit nitrification seems to be common in African perennial grasses and some crops (Lata et al., 2004, 2022; O'Sullivan et al., 2016; Rossiter-Rachor et al., 2009; Subbarao et al., 2009), little is known about the environmental conditions that have been selected for this behaviour (but see Lata et al., 2022). Even if this inhibition has not been assessed in other savanna types, mineral N partitioning could be involved in the tree–grass coexistence of all West African humid savannas that have virtually the same dominant grass and tree species as the Lamto savanna. The high performance of African grasses and their effects on N cycling in northern Australian and South American savannas (D'Antonio & Vitousek, 1992; Rossiter-Rachor et al., 2009) also seem to be related to their BNI ability. Although the frequency of this ability in other African grasses is not fully known (Lata et al., 2022), many African grasses appear to be able to inhibit nitrification, so that the new coexistence mechanism we emphasize should be studied at a large geographical scale and particularly in Eastern and Southern African savannas. Besides, N-fixing trees and large herbivores, which are absent in the Lamto savanna, are known to be influential in the functioning of other savannas such as East African savannas (Sankaran et al., 2008). These mechanisms, which provide important N inputs through symbiotic fixation, animal dung and urine, and impact N cycling differently, should be included in new models to assess the robustness of our results.

Clearly, our new mechanism of coexistence based on the partition of the mineral N resource probably interacts with formerly identified mechanisms based on the impact of disturbances on tree demography to explain tree–grass coexistence (Higgins et al., 2000). Although fire is determinant for the maintenance of savanna structure by reducing woody cover (Gignoux et al., 2006), mineral N partitioning likely acts in interaction with fire, as the intensity of fire depends on the biomass of flammable grasses, this grass biomass depending in turn on their N acquisition, essential nutriment for their growth. For example, nitrification inhibition by grasses has been shown to increase grass biomass, which should increase fire intensity and its capacity to impede tree encroachment. This would ultimately favour tree–grass coexistence. However, new models should be built to take into account mechanisms based on both resource competition and demography.

AUTHOR CONTRIBUTIONS

Sarah Konaré, Kouamé Fulgence Koffi, Simon Boudsocq, Jacques Gignoux, Jean-Christophe Lata, Xavier Raynaud and Sébastien Barot conceived the ideas and designed methodology. Sarah Konaré analysed the model and wrote the manuscript with the contribution of all co-authors. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

This a modelling paper. All data regarding the model are included in the paper.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Schematic representation of the two-patch model.

Appendix S2: Model parameters.

Appendix S3: Graphical representation of scenarios of invasion by trees versus invasion by grasses.

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

Appendix S5: Regular distribution.

Appendix S6: Effect of tree preference under their canopy depending on spatial tree distributions.

Appendix S7: Plant biomass depending on tree distributions.

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