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E-Article

Nitrification Control by Plants and Preference for Ammonium versus Nitrate: Positive Feedbacks Increase Productivity but Undermine Resilience

Alice Nadia Ardichvili,* Nicolas Loeuille, Jean-Christophe Lata, and Sébastien Barot

Sorbonne Université, Université de Paris-Cité, UPEC, CNRS, INRAE, IRD, UMR 7618, Institute of Ecology and Environmental Sciences, Paris, France

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ABSTRACT: Some plants, via their action on microorganisms, control soil nitrification (i.e., the transformation of ammonium into nitrate). We model how the covariation between plant control of nitrification and preference for ammonium versus nitrate impacts ecosystem properties such as productivity, nitrogen (N) losses, and overall resilience. We show that the control of nitrification can maximize productivity by minimizing total inorganic N losses. We initially predicted that plants with an ammonium preference should achieve the highest biomass when inhibiting nitrification, and conversely that plants preferring nitrate should achieve the highest biomass by stimulating nitrification. With a parametrization derived from the Lamto savanna (Ivory Coast), we find that productivity is maximal for plants that slightly prefer ammonium and inhibit nitrification. Such situations, however, lead to strong positive feedbacks that can cause abrupt shifts from a highly to a lowly productive ecosystem. The comparison with other parameter sets (Pawnee short-grass prairie [United States], intensively cultivated field, and a hypothetical parameter set in which ammonium is highly volatilized and nitrate inputs are high) shows that strategies yielding the highest biomass may be counterintuitive (i.e., preferring nitrate but inhibiting nitrification). We argue that the level of control yielding the highest productivity depends on ecosystem properties (quantity of N deposition, leaching rates, and baseline nitrification rates), not only preference. Finally, while contrasting N preferences offer, as expected, the possibility of coexistence through niche partitioning, we stress how control of nitrification can be framed as a niche construction process that adds an additional dimension to coexistence conditions.

Keywords: plant-soil feedback, nitrogen cycle, ecological dynamics, coexistence, biological inhibition of nitrification.

Introduction

Interactions between plants and microorganisms result in feedbacks between plants and local soil communities (Philippot et al. 2013). These feedbacks, by positively or negatively impacting plant growth and survival, influence the dynamics and functioning of plant communities (Klironomos 2002; Reynolds et al. 2003; Diez et al. 2010). For example, soil and water retention by perennial species in semiarid systems generate positive feedbacks causing patchy patterns of vegetation (Klausmeier 1999; Kéfi et al. 2007). Positive feedbacks due to enhanced nutrient acquisition (with nitrogen-fixing bacteria or fungal associations) may also lead to alternative stable states in population or community dynamics (Koffel et al. 2021). Associated tipping points can cause abrupt extinctions in response to increased stress (Jenerette and Wu 2004) or to priority effects (Adema et al. 2005; Lu and Hedin 2019).

Plant-soil feedbacks (PSFs) thus have important consequences for nutrient cycling. Moreau et al. (2019) reviewed how PSFs impact the dynamics of nitrogen (N), one of the principal factors limiting plant growth (Vitousek and Howarth 1991). Depending on local conditions, microorganisms compete with plants for N sources (He et al. 2021) or lead to mutualistic interactions facilitating plant N uptake (e.g., the mycorrhizal symbiosis). A well-studied example is the symbiotic fixation of N_2, which can be maintained even in N-rich ecosystems because of litter transfer between patches of fixers and nonfixers (Menge and Levin 2017).

Plants also positively or negatively control nitrification via root exudates affecting the metabolism of nitrifying bacteria and archaea (Lata et al. 1999, 2004, 2022; Srikanthasamy et al. 2018, 2021, 2022; Subbarao et al. 2007*a*, 2009). Crops

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* Corresponding author; email: alice.ardichvili@mail.mcgill.ca.

ORCIDs: Ardichvili, https://orcid.org/0000-0001-8057-2639; Loeuille, https://orcid.org/0000-0001-9588-6542; Lata, https://orcid.org/0000-0002-1094-4625; Barot, https://orcid.org/0000-0002-5910-538X.

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such as sorghum, rice, maize, wheat, and *Brachiaria* exude molecules that block the enzymes involved in the first step of nitrification (Zakir et al. 2008; Subbarao et al. 2009; Coskun et al. 2017). This negative control of nitrification is commonly called biological nitrification inhibition (BNI). Boudsocq et al. (2009) showed that nitrification inhibition increases primary productivity when the recycling efficiency of the ammonium pathway is higher than the recycling efficiency of the nitrate pathway. Some tree species in West African savannas (Srikanthasamy et al. 2018), temperate forests (Andrianarisoa et al. 2010), invasive grasses and forbs in American grasslands (McLeod et al. 2016), and wheat (He et al. 2022) can stimulate nitrification (positive control). Underlying mechanisms remain unclear, but this stimulation of nitrification could be due to the emission of specific root exudates and/or to the local modification of soil properties (e.g., due to litter stoichiometry, water content) that boosts nitrifier populations (Srikanthasamy et al. 2018; He et al. 2022). While these studies assess nitrification control for certain species, the consequences of nitrification control for ecosystem dynamics and functioning at a larger scale remain largely unknown (but see Konaré et al. 2019).

Plants grow from the absorption of both ammonium and nitrate, in proportions that depend on several factors (Britto and Kronzucker 2013). Following classical optimal foraging theory definitions (Pulliam 1974), we here define preference as the ability of plants to take up nitrate and ammonium in proportions that differ from their relative proportions in the soil. A meta-analysis suggests that grasses prefer nitrate while other functional groups (forbs, trees, shrubs) prefer ammonium (Yan et al. 2019). Among different populations of several grass species in Africa, Wang and Macko (2011) showed that preferences vary among plant species. Boudsocq et al. (2012) showed that variations in plant preference strongly impacts ecosystem productivity and N losses of the ecosystem, the preference yielding highest biomass being slightly biased toward ammonium. At the community level, available ammonium versus nitrate offers possibilities of niche partitioning and may explain the coexistence of plants with contrasting preferences (Boudsocq et al. 2012; Konaré et al. 2019). On top of niche separation due to preference, nitrification control also results in niche construction (i.e., modification of the local environment), with important consequences for species coexistence (Odling-Smee et al. 1996).

Plant preference for ammonium versus nitrate and control of nitrification are likely to feed back on each other. Plants that inhibit nitrification will benefit from this niche construction only if they prefer ammonium. Conversely, nitrification activation will enhance plant growth only if it prefers nitrate. As such, control of nitrification can be viewed as an effect trait and preference as a response trait (sensu Lavorel and Garnier 2002). We here show that simultaneously accounting for nitrification control and preference offers new insights regarding the productivity, resilience, and coexistence conditions within ecosystems. We highlight the joint effect of preference for ammonium versus nitrate and control of nitrification and (i) its implications for the ability of a plant population to colonize and its resilience (ability to recover after a perturbation; Holling 1973) once established, (ii) its impacts on ecosystem productivity, and (iii) the respective influence of niche differentiation and niche construction for the coexistence of plant species competing for N. Positive feedbacks have important consequences for ecosystem dynamics, in particular for the persistence and resilience of ecosystems (van Nes et al. 2016). With respect to question i, we therefore expect that the combination of control of nitrification and plant preference may generate positive feedbacks that undermine the resilience of plant populations. We suspect that the establishment of such feedbacks may strongly depend on ammonium and nitrate relative leaching rates. With respect to question ii, we predict an enhancement of plant biomass when control of nitrification enhances the preferred form of N in the soil. Ammonium specialists should therefore achieve higher biomass when inhibiting nitrification, while nitrate specialists should achieve higher biomass when stimulating nitrification. Following previous findings (Boudsocq et al. 2009), we expect that nitrification control may enhance conservation of N in the system (i.e., minimize N losses), thereby increasing productivity. With respect to question iii, we hypothesize that when a species helps another species by creating its niche (e.g., a nitrification-stimulating plant helps a nitrate specialist), the facilitating effect between the two species promotes coexistence (Kylafis and Loreau 2011). On the other hand, if two competing species create their own niche (e.g., a nitrate specialist stimulates nitrification while an ammonium specialist inhibits nitrification), the resulting negative interspecific effect should lead to priority effects and undermine coexistence (Tilman 1980). To test these hypotheses, we compared all combinations of preference for nitrate versus ammonium and control of nitrification in four ecosystems with contrasted N fluxes. Contrary to former published models (Boudsocq et al. 2009, 2012), we include the possibility of a cost of the control of nitrification and use a more realistic function linking plant biomass to its impact on nitrification.

Methods

Our model is based on the equations of Boudsocq et al. (2009, 2012) and describes the dynamics of N in four compartments: plants (P), detritus (D), ammonium (N_A), and nitrate (N_N; fig. 1). We assume that plants are only limited by N, so that more available N leads to more plant growth. We assume that plant biomass is proportional to plant N

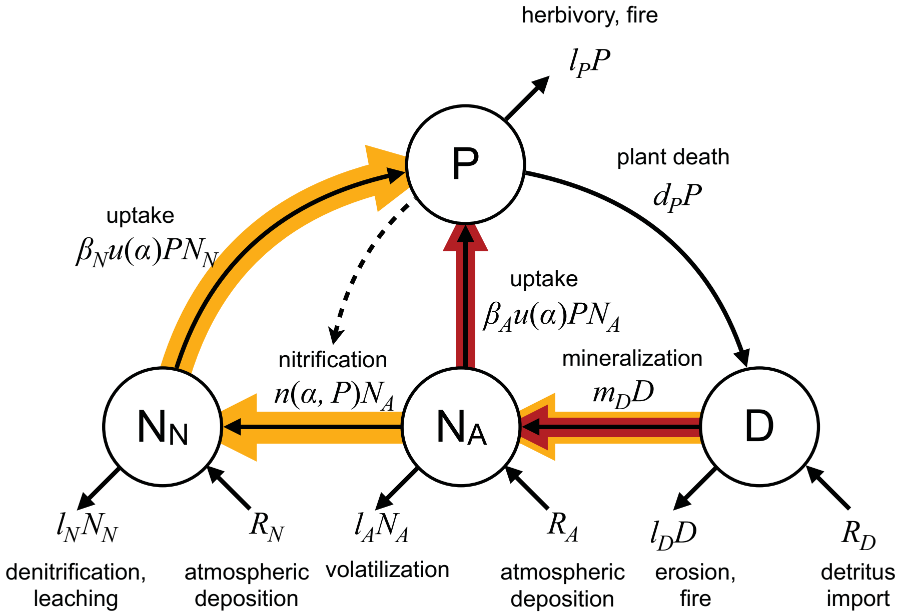

Figure 1: Model of the N cycle in an ecosystem through plants (P), detritus (D), ammonium (N_A), and nitrate (N_N). Fluxes between stocks are solid arrows. The dotted arrow illustrates plant nitrification control. Definitions and default values of parameters are presented in table 1. Two possible recycling pathways appearing in equation (7) are illustrated with thick arrows. Orange: first recycling loop—N travels only through the detritus (D), ammonium (N_A), and plant (P) compartments. Yellow: second recycling loop—N travels through both the ammonium compartment (N_A) and the nitrate compartment (N_N) in addition to the plant (P) and detritus (D) compartments.

content (i.e., that the C∶N ratio is fixed) and refer to the size of the plant N compartment as plant biomass for simplicity.

The dynamics of N in the ecosystem are described by the following differential equations:

$$\frac{dP}{dt} = (\beta_A u(\alpha)N_A + \beta_N u(\alpha)N_N - d_P - l_P)P, \tag{1}$$

$$\frac{dD}{dt} = R_D + d_P P - (m_D + l_D)D, \tag{2}$$

$$\frac{dN_A}{dt} = R_A + m_D D - \beta_A u(\alpha)PN_A - n(\alpha, P)N_A - l_A N_A, \tag{3}$$

$$\frac{dN_N}{dt} = R_N + n(\alpha, P)N_A - \beta_N u(\alpha)PN_N - l_N N_N. \tag{4}$$

N enters the system via the ammonium N_A and nitrate N_N pools by atmospheric deposition or via the D pool by detritus import (parameters R_A, R_N, and R_D, respectively). N can also be lost from the plant compartment P at a rate l_p due to fire or herbivory, from the detritus compartment D at a rate l_D due to fire or erosion, from the N_A compartment at a rate l_A by volatilization, and from the N_N compartment at a rate l_N by denitrification and leaching. N is recycled as plant parts die and join the detritus compartment at a rate d_p, detritus is mineralized at a rate m_D, and ammonium is nitrified at a rate n, which is modified by the control of nitrification by plants. This control depends on per biomass investment in control of nitrification α and on plant biomass P (eq. [5]; fig. 2):

$$n(\alpha, P) = n_{\max} \frac{e^{\alpha P}}{e^{\alpha P} - 1 + \dfrac{n_{\max}}{n_0}}. \tag{5}$$

When there are no plants ($P = 0$) or when plants do not invest in control ($\alpha = 0$), ammonium is nitrified at a constant baseline rate n_0. When $\alpha < 0$, plants inhibit nitrification, so that n decreases with plant biomass, asymptotically reaching zero. When $\alpha > 0$, plants stimulate nitrification and n increases with plant biomass, asymptotically reaching a maximum nitrification rate $n_{\max}$. Such a bounded, nonlinear shape avoids situations where nitrification rates can increase to infinity when plants stimulate nitrification. Plants take up N from the ammonium and nitrate compartments at a baseline rate u. Uptake from each compartment depends on plant preference for ammonium and nitrate, β_A and β_N, with $\beta_A + \beta_N = 1$. Ammonium uptake is $\beta_A u N_A$, and nitrate uptake is $\beta_N u N_N$; note that when $\beta_A = \beta_N$, the proportion of ammonium (resp. nitrate) consumed by

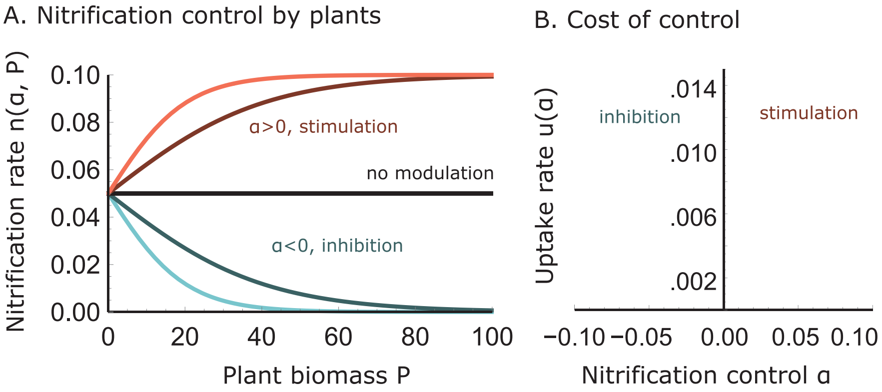

Figure 2: *A*, Nitrification rate as a function of plant biomass, for different levels of control (α values of −0.1, −0.05, 0, 0.05, 0.1). $n_0 = 0.05$, $n_{\max} = 0.1$ *B*, The N uptake rate decreases as plants allocate more energy to controlling nitrification. The uptake rate is plotted with $u_{\max} = 0.01336$ and $v = 0.05$.

the plant is $N_A/(N_A + N_N)$ (resp. $N_N/(N_A + N_N)$). Plants then consume N forms exactly according to their availability, which corresponds to the "no-preference" scenario. Conversely, an ammonium specialist has a strong preference for ammonium ($\beta_A \gg \beta_N$), while a nitrate specialist has a strong preference for nitrate ($\beta_N \gg \beta_A$). We assume that the production of root exudates responsible for nitrification control is energetically costly for plants, so that the uptake rate u also depends on α (fig. 2):

$$u(\alpha) = u_{\max} e^{-(\alpha/v)^2}. \tag{6}$$

Parameter u is maximal when plants do not control nitrification ($\alpha = 0$) and decreases as plants inhibit or stimulate nitrification. Parameter v determines the strength of the cost of nitrification control. A list of parameters is provided in table 1.

When mathematical analysis of the model is not possible, we numerically investigate the system using four baseline sets of parameters: the Lamto savanna (Ivory Coast; Boudsocq et al. 2009), the Pawnee short-grass prairie (United States; Woodmansee et al. 1978), a modified version of the Lamto set to mimic an intensively cultivated field, and a hypothetical parameter set (labeled "high nitrate"). While few well-documented N budgets exist for herbaceous ecosystems, the Lamto savanna and Pawnee prairie contrast in various ways that are interesting for our general objective. Grasses (*Poaceae*) inhibit nitrification in the Lamto savanna, while they do not control nitrification in Pawnee. The two systems also largely vary in their baseline and maximum nitrification rates (lower in Pawnee than in Lamto). Inputs are larger in Lamto than in Pawnee, as are losses of ammonium and nitrate. We hypothesize that these four parameters determine the strength of positive feedbacks, which depends on the quantity of N recycled along such loops, and are therefore directly dependent on N inputs and losses. We also modify the Lamto parameter set to mimic an agricultural system. Inputs of organic N (R_D) may represent manure fertilization. Inorganic inputs are increased to model an ammonium-nitrate application of 100 kg N/ha/yr (Einarsson et al. 2021). Baseline and maximum nitrification rates are increased to mimic empirical observations in agricultural systems (Elrys et al. 2021). Finally, to test our hypothesis that inputs, losses, and baseline or maximum nitrification rates drive the establishment of positive feedbacks, we investigate a hypothetical model based on Lamto parameters, with inverted inorganic inputs and loss rates ($R_N > R_A$ and $l_A > l_N$) and increased maximum nitrification rate. Ammonium losses larger than nitrate losses are unrealistic in most ecosystems (although they may accurately reflect high volatilization rates in alkaline soils); this high-nitrate parameter set serves solely to test our hypothesis.

To study the effect of nitrification control and preference on ecosystem dynamics and resilience (question i) and functioning (question ii), we determine the expression of the compartment equilibria by setting the system of differential equations to zero. We evaluate the Jacobian matrix at equilibria to determine the conditions of stability of the system. For the two parameter sets and in a range of α and β_A values, we numerically solve the differential equations to obtain all equilibrium values and their stability. We chose an interval for α values (from −0.125 to 0.125 with an increment of 0.001) sufficiently large to cover a complete range of outcomes, from maximally productive systems to plant extinction. We varied β_A from 0 to 1 (with an increment of 0.01) to capture all possible strategies. A meta-analysis shows that on average forbs strictly depend on ammonium ($\beta_A = 1$; Yan et al. 2019), and other experimental work suggests

Table 1: Variables, parameters, units, and default values

Symbol	Meaning	Unit	Pawnee[a]	Lamto[b]	Cultivated field	High-nitrate model
Variables:						
t	Time	yr				
P	N content of plants	kg ha^{-1}				
D	Detritus N content	kg ha^{-1}				
N_A	Soil ammonium content	kg ha^{-1}				
N_N	Soil nitrate content	kg ha^{-1}				
Parameters:						
d_P	Plant recycling rate	yr^{-1}	.258	.6	.6	.6
l_P	Plant loss rate	yr^{-1}	0	.4	.4	.4
R_D	Annual inputs of detritus	kg ha^{-1} yr^{-1}	0	16	16	16
m_D	Mineralization rate	yr^{-1}	.01338	.025	.025	.025
l_D	Detritus loss rate	yr^{-1}	.01338	.0027	.0027	.0027
$u_{\max}$	Maximum uptake rate	yr^{-1}	.136	.14186	.14186	.14186
R_A	Annual inputs of ammonium	kg ha^{-1} yr^{-1}	3	23	50	4.1
l_A	Ammonium loss rate	yr^{-1}	.05	.0133	.0133	2.7
R_N	Annual inputs of nitrate	kg ha^{-1} yr^{-1}	3	4.1	50	23
l_N	Nitrate loss rate	yr^{-1}	.15	2.7	2.7	.0133
n_0	Nitrification rate in the absence of plants	yr^{-1}	.05	2.7	5	2.7
$n_{\max}$	Maximum nitrification rate	yr^{-1}	.1	4.16	10	27
α	Strength of control of nitrification	kg^{-1} ha				
v	Cost of nitrification control	kg^{-1} ha	.5[c]	.05[c]	.05[c]	.05[c]
β_A	Plant preference for ammonium					
β_N	Plant preference for nitrate					

[a] From Woodmansee et al. 1978.

[b] From Boudsocq et al. 2009.

[c] Except v, which has not been estimated in the ecosystems. For a discussion on the value of v, see supplement H.

that plants of the *Brassicaceae* or *Poaceae* family have a preference of 0.1 (Errebhi and Wilcox 1990). With respect to question i, we expect that nitrification control and preference for ammonium or nitrate can generate positive feedbacks and that the stability conditions to vary with α and β_A. With respect to question ii, we study how the equilibrium plant biomass P^* varies with α and β_A, expecting two local maxima in the α and β_A plane—one corresponding to the ammonium specialist that inhibits nitrification, the other to the nitrate specialist that stimulates nitrification. We also study how total inorganic N losses ($l_A N_A^* + l_N N_N^*$) vary with respect to P^* to test the hypothesis that higher productivity is achieved by minimizing N losses. We assume that a positive and stable equilibrium exists and use equilibrium conditions (eqq. [1]–[4] set to zero) to implicitly differentiate equilibrium compartments values with respect to α. To address question iii—that is, the coexistence of different strategies—we test the mutual invasibility of two plants, P_1 and P_2, characterized by their nitrification control and their preference for ammonium. We compute the per capita growth rate of a rare $P_1(\alpha_1, \beta_{A1})$ (then $P_2(\alpha_2, \beta_{A2})$) in a system where $P_2(\alpha_2, \beta_{A2})$ (then $P_1(\alpha_1, \beta_{A1})$) is at its equilibrium (equations of the two-plant system are presented in supplement A; supplements A–H are available online). When the per capita growth rate of a plant species is positive, it is possible for that species to invade the other. If both species can invade one another, it is supposed that coexistence is maintained in the long term (Armstrong and McGehee 1980).

All analyses (Ardichvili 2023) are done using Wolfram Mathematica 12.2 (Wolfram Research 2021) and R 4.2.2 (R Core Team 2018).

Results

Condition of Existence of the Plant Population

There are two possibly stable equilibria: the plant is either extinct (and soil compartments stabilize at values given in supplement B) or reaches a positive equilibrium that has no clear analytical expression. We investigate the conditions of existence of the plant population by deriving the conditions under which plants can colonize an empty environment.

Initial colonization is possible when the null equilibrium is unstable, which occurs when nitrification control and preference meet the following conditions:

$$u(\alpha) > \frac{d_P + l_P}{\beta_A\left(\frac{1}{l_A + n_0}\left(R_A + \frac{m_D R_D}{l_D + m_D}\right)\right) + \beta_N\left(\frac{1}{l_N}\left(R_N + \frac{n_0}{l_A + n_0}\left(R_A + \frac{m_D R_D}{l_D + m_D}\right)\right)\right)}. \tag{7}$$

Note that nitrification control, α, does not directly appear in equation (7). It appears only in the left-hand part of equation (7) in the uptake function $u(\alpha)$. Since $u(\alpha)$ is a decreasing function of α, nitrification control only undermines the establishment of plants. Indeed, the strength of control depends on plant biomass, which is close to zero at the moment of colonization. In small populations, plants pay only the cost of controlling without experiencing its potential benefits. As a corollary, based on equation (7), controlling plants ($\alpha \neq 0$) can invade when the cost v associated with control is sufficiently low.

In the denominator of the right-hand side, two recycling pathways appear (fig. 1). The term in the first bracket $1/(l_A + n_0)(R_A + m_D R_D/(l_D + m_D)$ corresponds to the efficiency of the ammonium pathway (orange in fig. 1), while the second bracket $1/l_N(R_N + n_0/(l_A + n_0)(R_A + m_D R_D/(l_D + m_D)))$ is the efficiency of the full recycling pathway (ammonium plus nitrate; yellow in fig. 1; see supplement C for more details). Inputs from the soil compartment have to be well recycled along those two pathways for the plant population to be able to colonize an empty patch. The importance of the two pathways is weighted by the ammonium versus nitrate preference of the plant. Considering an ammonium specialist ($\beta_A \approx 1$ and $\beta_N \approx 0$), only the ammonium pathway determines whether the plant can successfully colonize. Considering a nitrate specialist ($\beta_A \approx 0$ and $\beta_N \approx 1$), the complete pathway matters. The main asymmetry between an ammonium specialist and a nitrate specialist is that the ammonium specialist is not affected by the dynamics of the nitrate compartment, whereas the nitrate specialist is affected by the recycling efficiency in the ammonium compartment.

Positive Feedbacks Associated with Nitrification Control May Generate Alternative Stable States

We now study the implications of nitrification control and preference for ammonium versus nitrate with respect to the resilience of a plant population that is already established. In some cases, the system can exhibit alternative stable states (e.g., Lamto parametrization in fig. 3). In a range of α and β_A values, the positive and the null equilibria are simultaneously stable. In that range of parameters, plants can exist but not invade due to the Allee effect caused by control of nitrification. This bistability implies that a highly productive ecosystem can abruptly shift to an unproductive (barren-like) state in response to a perturbation. For example, starting in a productive system with ammonium specialists grasses that strongly inhibit nitrification (point G in fig. 3), a perturbation (i.e., overgrazing) that would decrease plant biomass past a certain threshold T (black arrow in fig. 3), would lead to a collapse to a stable barren state (point B in fig. 3). Such bistability is associated with strong positive feedbacks (Scheffer et al. 2001). Here, higher biomass of a nitrification-inhibiting plant favors the accumulation of ammonium, which in turn favors higher plant biomass and higher inhibition. The positive feedback sustains high productivity or triggers a vicious circle: low accumulation of ammonium then decreases the density of plants, which no longer retain ammonium to the point where insufficient resources cause the extinction of the plants.

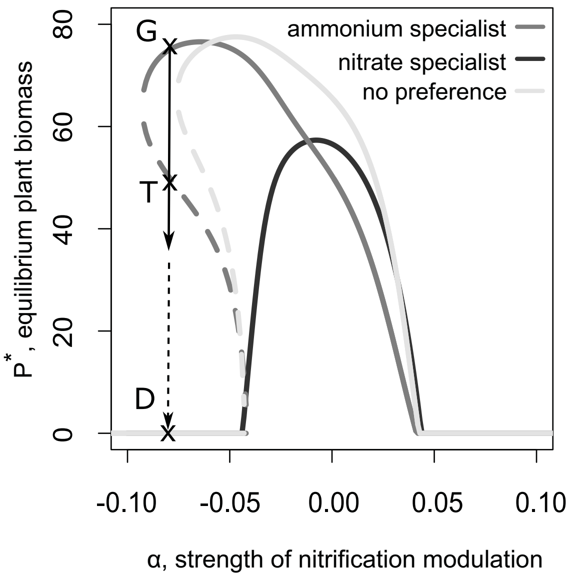

Figure 3: Nitrification control generates a potential for abrupt transitions between a productive state and a barren state (Lamto parametrization). For a nitrate specialist ($\beta_A = 0.1$ and $\beta_N = 0.9$), there is only one stable equilibrium (solid line) for any value of α, the strength of nitrification control. For an ammonium specialist ($\beta_A = 0.9$ and $\beta_N = 0.1$) or a generalist ($\beta_A = 0.5$ and $\beta_N = 0.5$), a range of α values leads to alternative stable states, separated by an unstable equilibrium (dashed line). This implies that a system in a productive state (G) can abruptly shift to a barren state (B) when a perturbation (black vertical arrow) crosses the unstable equilibrium (T).

Such bistability is present over a combination of nitrification control and preferences and for different parameterizations (fig. 4). With the Lamto parametrization, bistability is possible for ammonium-consuming plants that inhibit nitrification (fig. 4*A*). With Pawnee parameters, only restricted combinations of preference and control

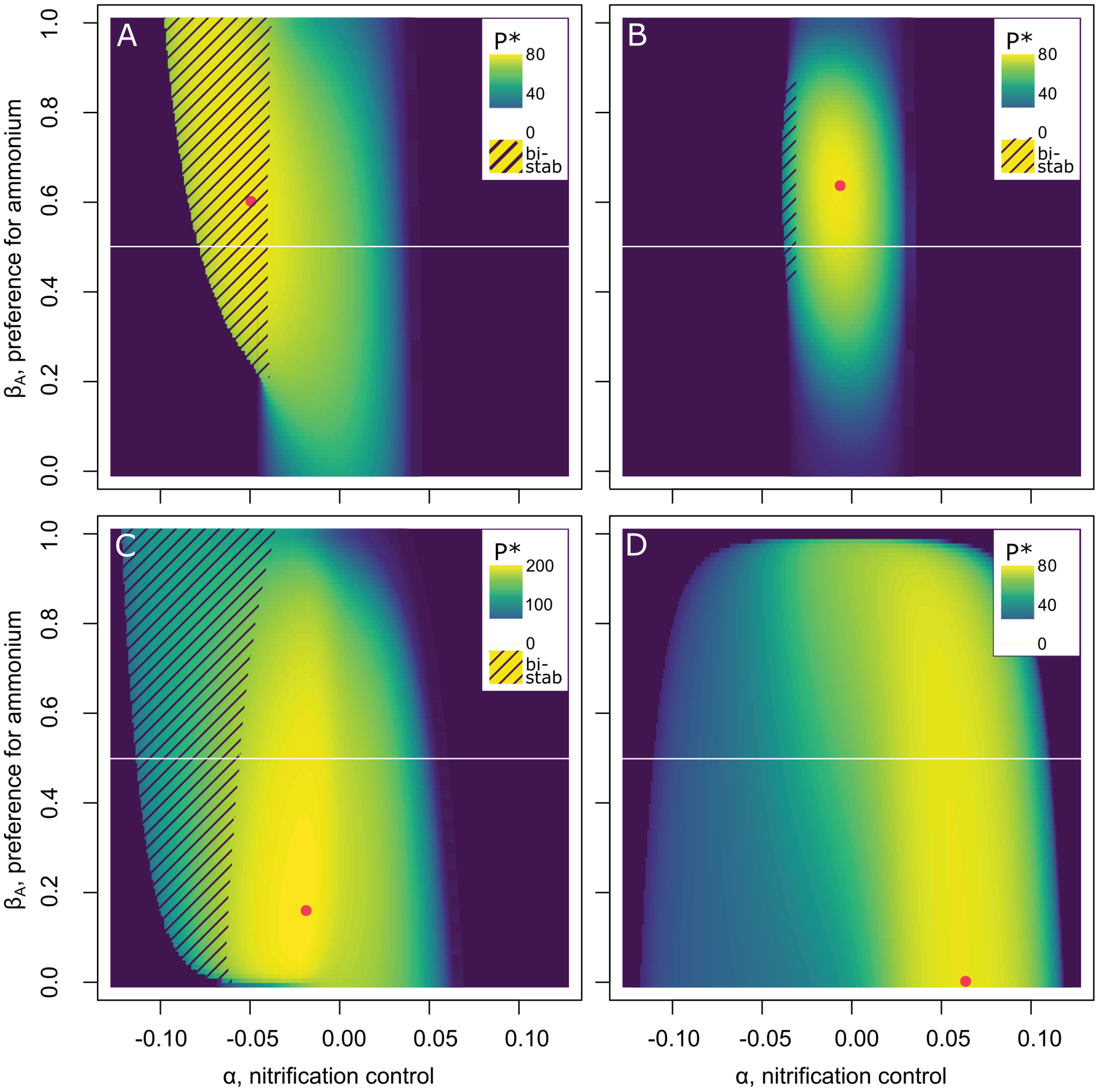

Figure 4: Effect of preference for ammonium versus nitrate and nitrification control on plant biomass for the Lamto (*A*), Pawnee (*B*), cultivated (*C*), and high-nitrate (*D*) parametrization. Color indicates the production of biomass from dark purple (production = 0 kg/ha) to yellow (production = 80 kg/ha). Areas with alternative states (one productive, one unproductive, as in fig. 3) are hatched. Parameter combinations that support the maximum biomass are indicated by a red circle. Biomass of plants that do not have a preference is read along the white horizontal line.

lead to alternative stable states (fig. 4*B*). With the cultivated system parametrization, bistability occurs for many nitrification-inhibiting strategies, regardless of their preference (fig. 4*C*). Finally, against our expectations, there is no bistability for the high-nitrate parametrization (fig. 4*D*). In cases where plants do not show any preference, alternative stable states exist with the Lamto and cultivated set but not with Pawnee's.

Elasticity analysis of the size of the bistability region (supplement D) confirms that bistability depends on parameters involved in the feedback loop. With the Pawnee parameter set, increased ammonium inputs (R_A) result in a larger flux from the ammonium compartment to the plant compartment, resulting in a stronger feedback loop that increases the area of bistability (supplement D). Decreased ammonium inputs would have a reverse, but symmetrical, effect. Similarly, the maximum uptake rate ($u_{\max}$) and the mortality rate of plants (d_P) affect the fluxes from ammonium to plants and from plants to detritus, respectively, and are the most influential parameters on bistability with the Pawnee parametrization. With the Lamto parameter set, bistability is mostly influenced by inputs of ammonium (R_A), the baseline nitrification rate (n_0), and losses from the plant compartment (l_P). Note that alternative stable states can also be observed, even when control of nitrification is costless (supplement H2).

We investigate how nitrification control and preference for ammonium versus nitrate impact ecosystem productivity. Figure 4 shows that plant biomass is affected in different ways by the four parameterizations. Consistent with equation (7), the direct cost of control limits the existence of plants (purple areas on the side of each panel in fig. 4). For the Lamto and high-nitrate parametrization, our results are partially consistent with our expectations: biomass production is maximal for plants that create their own niche, that is, nitrification-inhibiting ammonium specialists with Lamto parameters (fig. 4*A*) and nitrification-stimulating nitrate specialist with high-nitrate parameters (fig. 4*D*). What is striking, however, is that no parametrization led to the expected two maxima for the two niche-building strategies. In the cultivated system (fig. 4*C*), biomass production is maximal for a seemingly counterintuitive strategy, nitrate specialists that inhibit nitrification, while in Pawnee maximal biomass production occurs for plants that prefer ammonium and do not control nitrification. For plants that do not have a preference (i.e., taking a horizontal transect along $\beta_A = 0.5$; white line in fig. 4), the highest biomass occurs for nitrification-inhibiting plants for Lamto and the cultivated system, for plants that do not control nitrification with Pawnee parameters, and for plants that stimulate nitrification with the high-nitrate parameter set. In addition, strikingly, with the Lamto parametrization, plant biomass is highest when alternative stable states exist. Highly productive systems also overlap with the bistability region in the cultivated parametrization (fig. 4*C*). This implies that highly productive strategies may also be the least resilient.

Plant Biomass Is Maximal When N Losses Are Minimal

We now investigate the link between productivity and N leaching and how these two ecosystem processes vary with nitrification control. Rearranging the implicit differentiations of equations (1)–(4) set to zero (supplement E), we obtained the following expression of how total N losses vary with control of nitrification:

$$\frac{\partial(l_A N_A^* + l_N N_N^*)}{\partial\alpha} = \frac{\partial P^*}{\partial\alpha}\left(\left(\frac{m_D}{l_D + m_D}\frac{d_P}{l_p + d_P} - 1\right)(l_P + d_P)\right). \tag{8}$$

The term $m_D/(l_D + m_D)d_P/(l_P + d_P) - 1$ is negative, meaning that P^*, equilibrium plant biomass, has the opposite variations of the total N losses ($l_A N_A^* + l_N N_N^*$) with respect to α. In other words, inhibition of nitrification increases ecosystem productivity by minimizing total N losses. In figure 4, N losses are maximal in the blue area and minimal in yellow parts of the plot.

Control of Nitrification Modifies Coexistence Conditions

We expected that coexistence between two plant species (P_1 and P_2) characterized by different preferences and controls would be possible when (i) species have well-contrasted preferences (niche partitioning) or (ii) nitrification control builds the other species niche, resulting in a facilitating effect. In contrast, if the two species build their own niche (e.g., a nitrate specialist stimulates nitrification while an ammonium specialist inhibits nitrification), the resulting negative interspecific effect should lead to priority effects and undermine coexistence. Figure 5 shows the results of the mutual invasions between P_1, which has the strategy located at the purple star, and a range of alternative P_2 combinations of nitrification control and preference for ammonium, for two strategies in the Pawnee and Lamto parameterizations. Other P_1 strategies are investigated in supplement F, as are the cultivated and high-nitrate parameterizations. Within a given panel of figure 5, coexistence by niche differentiation can be read along the vertical axis, which corresponds to preference for ammonium of P_2. In figure 5*C*, for instance, drawing a vertical line through point a, coexistence is possible with species b_1, an ammonium specialist, because its niche is sufficiently different from point a. Whenever coexistence is possible for species that are opposed on the vertical axis, coexistence is explained by niche differentiation.

Coexistence by facilitation via niche construction can be read from the asymmetry between the left and right halves of each panel, which corresponds to variations in nitrification control by P_2. Again, in figure 5*C*, species a can coexist with species b_2 and not with species b_3. Species b_2 and b_3 have similar preferences for nitrate, implying that niche differentiation is equally weak for the pairs of species a-b_2 and a-b_3. Species b_2, however, stimulates

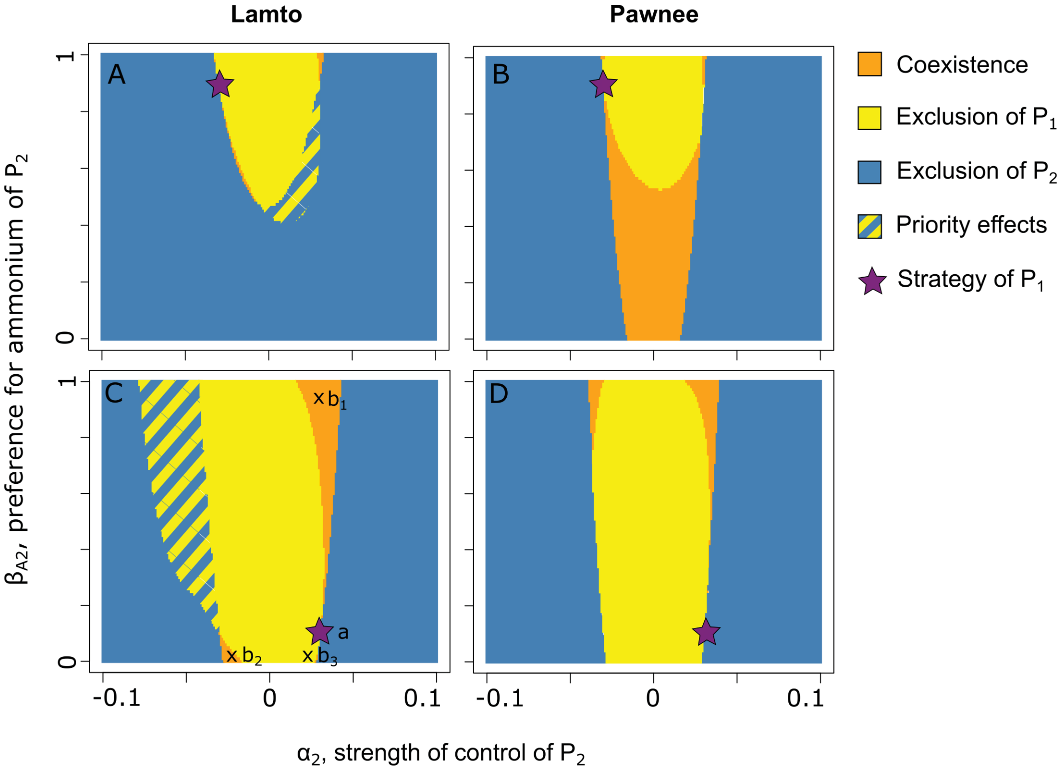

Figure 5: Results of the mutual invasion of two plant species P_2 and P_1 for a fixed P_1 strategy for the Lamto (*A*, *C*) and Pawnee (*B*, *D*) parametrizations. In *A* and *B*, P_1 is an inhibiting ammonium specialist; in *C* and *D*, P_1 is a stimulating nitrate specialist. Whenever coexistence is possible for species that are opposed on the vertical axis (as exemplified by species a and b_1 in *C*), coexistence is explained by niche differentiation. Coexistence by facilitation via niche construction can be read from the asymmetry between the left and right halves of the panel (as exemplified by species b_2 and b_3 in *C*).

nitrification, which promotes the growth of the nitrate specialist species a, while species b_3 inhibits nitrification, which suppresses the niche of species a. Coexistence is possible only for the facilitating interactor species b_2. When species a is facilitated by species b_2, its soil allows an increased availability of ammonium that favors species b_2 and stable coexistence. In figure 5, Lamto and cultivated panels (fig. 5*A* and 5*C*, respectively) are more asymmetrical along the vertical axis than those of Pawnee and high nitrate (fig. 5*B* and 5*D*, respectively). A more complete observation of different P_1 strategies (see supplement F) hints that niche construction plays less of a role in mediating coexistence with Pawnee parameters than in the other sets, which may be explained by the fact that nitrification with Pawnee parameters is not allowed to reach high values (table 1).

The joint effect of niche differentiation and niche construction may be responsible for priority effects (neither species can invade when the other is present; stripped areas in fig. 5*A*, 5*C*). Supplement D shows that these tend to occur when species build their own niche (nitrate specialists stimulating nitrification and species having a greater preference for ammonium and inhibiting nitrification, and conversely).

Discussion

We modeled the dynamics of N in a four-compartment model to study the joint effect of nitrification control and plant preference for ammonium versus nitrate on plant dynamics, productivity, and coexistence. Jointly varying plant preference and control of nitrification yielded new insights relative to studying the two traits separately, as was done in Boudsocq et al. (2009, 2012), as these two dimensions interact in complex ways. Nitrification control and preference can generate positive feedbacks that potentially maximize plant productivity by minimizing N losses but also create conditions of low resilience and abrupt shifts between contrasted ecosystem productivities. Plants with different preferences and different strengths of control can coexist when their preferences are sufficiently different and/or their control activity creates the niche of the other species (i.e., enhancing the preferred source of N). The comparison of four parameter sets shows that external fluxes such as inputs or outputs determine which strategies lead to maximal productivity.

Nitrification Control and Ammonium versus Nitrate Preference Constrain the Existence and Resilience of Plant Populations

The niche construction activity of plants opens an "Allee niche" in which plants can exist but not invade (Koffel et al. 2021). Contrary to our expectations, the only strategies leading to bistability were the inhibitors in Lamto and the cultivated system. We did not find the expected bistability for nitrate specialists that stimulate nitrification, even in a high-nitrate ecosystem. A likely explanation resides in the high ammonium loss rate in the high-nitrate parametrization. This high loss decreases the overall efficiency on the full pathway (yellow in fig. 1) on which the nitrate specialist relies (eq. [7]). Figure 6 provides an illustration of how a strong positive feedback can be established in Lamto (larger fluxes from ammonium to plants, plants to detritus, and detritus to ammonium when the plant is inhibiting nitrification) and not in Pawnee, where the baseline nitrification rate is already small and inputs of ammonium are weak.

Alternative stable states imply that the ecosystem may respond in an abrupt, unpredictable, and nonlinear way to a perturbation (van Nes et al. 2016). In our case, biomass suppression due to fire or herbivory past a certain threshold could lead to a collapse of the system to a barren, grassless state (with the once-dominating plant extinct). The collapsed system may then be invaded by alternative species differing in their N niche. This result is reminiscent of empirical observations in some West African savannas, where the overgrazing of perennial, nitrification-inhibiting plants lead to their replacement by annual grasses that do not control nitrification (César 1992; Yé et al. 2017) and to a much lower primary production than perennial grasses. However, fire occurs frequently in such savannas, but no collapse to a barren state has been observed. A possible explanation lies in the local adaptation of plants to fire (Koffi et al. 2019). Note also that alternative stable states exist only over a given range of combinations of inhibition and preference

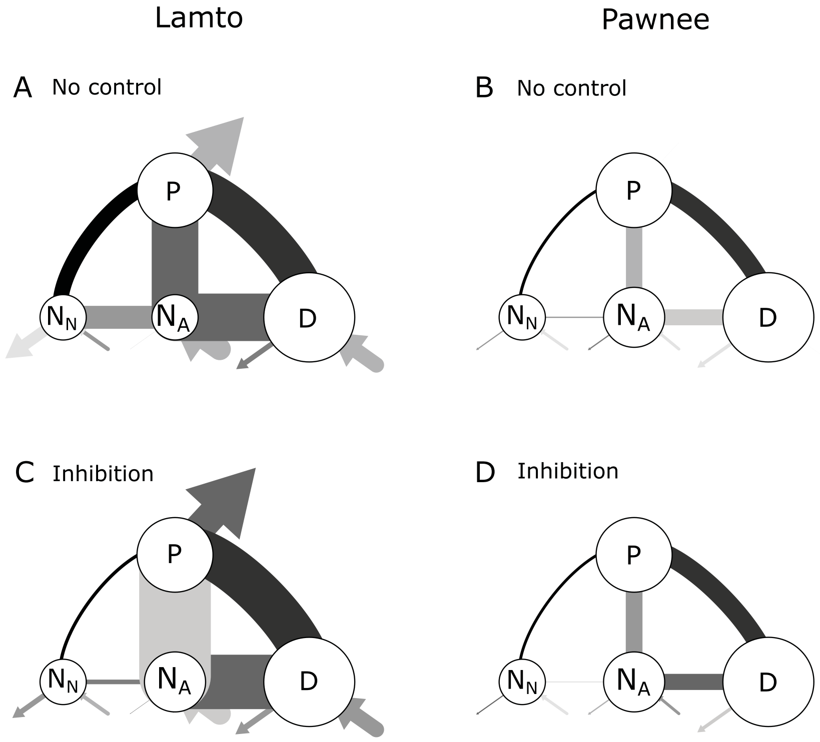

Figure 6: Impact of inhibition of nitrification on fluxes with Lamto (*A*, *C*) and Pawnee (*B*, *D*) parameters. Line width is proportional to flux size. Different shades are used for visualization purposes but have no meaning. *A*, *B*, Plants do not control nitrification. In Pawnee, the nitrification rate is low, whereas it is larger in Lamto. Inhibition of nitrification in Lamto (*C*) strongly reduces the nitrification rate, which promotes recycling via the ammonium pathway; this decreases N losses, creating a positive feedback loop. In contrast, Pawnee plants do not have much room for modifying the nitrification rate; the impact of inhibition in Pawnee is minor (*D*). *A*, $\alpha = 0$, $\beta_A = \beta_{A_{\rm opt}} = 0.6$. *B*, $\alpha = 0$, $\beta_A = \beta_{A_{\rm opt}} = 0.63$. *C*, $\alpha = \alpha_{\rm opt} = -0.049$, $\beta_A = \beta_{A_{\rm opt}} = 0.6$. *D*, $\alpha = \alpha_{\rm opt} = -0.005$, $\beta_A = \beta_{A_{\rm opt}} = 0.63$.

in our model, and the Lamto grasses may also be out of this range. A third hypothesis is that fire destroys only aboveground biomass, about one-third of total plant biomass (Yé et al. 2021), which may be insufficient to cause the collapse. Finally, the control could be plastic, which could change the modeled dynamics, for example if control is downregulated when the availability of ammonium decreases (Subbarao et al. 2007*b*). Interestingly, while the increase of atmospheric deposition of NH_4^+ due to agricultural pollution may increase plant productivity (van den Berg et al. 2016), our results suggest that higher rates of atmospheric deposition of NH_4^+ could increase the possibilities of tipping points to a barren state.

Control of Nitrification, Leaching, and Productivity

Productivity as well as N leaching largely vary with the control of nitrification. Previous results showed that nitrification inhibition increases primary productivity when the recycling efficiency of the ammonium pathway is higher than the recycling efficiency of the nitrate pathway (Boudsocq et al. 2009). Using a bounded, nonlinear control function and letting plant preference vary, we complement that finding by showing that nitrification control can increase plant productivity when N leaching is minimized, even when a cost to the control of nitrification is taken into account. This supports findings and theories suggesting that ecosystem processes and evolution tend to minimize losses of nutrient (Vitousek and Reiners 1975; Boudsocq et al. 2011; Menge et al. 2012).

Contrary to our expectations, we do not find two local maxima in plant productivity for nitrate specialists that stimulate nitrification and ammonium specialists that inhibit it. In most natural systems, because of the high leaching capacity of nitrate, no positive feedback leading to high productivity can exist for nitrification-stimulating nitrate specialists. In such systems, in the short term stimulating nitrification may increase resource availability for a nitrate specialist, but in the long term the low efficiency of the nitrate recycling loop is detrimental to fertility and the growth of such nitrification-stimulating plants. In comparison, with the high-nitrate parameter set in which we let ammonium losses be much larger than nitrate losses, highest productivity occurs for a nitrification-stimulating plant. As for the preference, with Lamto and Pawnee parameter sets, highest productivities occur for plants that have a slight preference for ammonium. This result is intuitive for Lamto, since inputs of ammonium are larger than inputs of nitrate. However, in Pawnee, where inorganic inputs are equal, the highest productivities may occur for plants that prefer ammonium because of the inherent asymmetry of the N cycle: ammonium is the first mineral that is produced by mineralization. In a system where inputs are much larger and the nitrification rate larger (as in the cultivated parametrization), the highest productivity occurs for plants preferring nitrate. The local maximum occurs for inhibitors with Lamto and cultivated parameters and plants that do not control nitrification with Pawnee parameters. The difference is largely driven by the baseline nitrification rate (fig. 6; supplement G). In Pawnee, the nitrification rate is low even when plants do not control nitrification (0.05 vs. 2.7 yr^{-1} in Lamto). Inhibiting plants in Pawnee also do not have a strong effect on the nitrification rate; hence, the benefits of niche creation by inhibition are outweighed by the costs.

Our choice of these ecosystems as baseline parameter sets thereby illustrates how nitrification control and its consequences highly differ among ecosystems. In some ecosystems (here, Lamto and the cultivated field), plants potentially exert large controls on nitrification, which may lead to high productivity but low resilience. In contrast, for others (here, Pawnee), control is limited because of external conditions, so that nitrification control exerts little influence on the overall functioning (fig. 6). The comparison between Lamto, Pawnee, a cultivated field, and a hypothetical ecosystem shows that the impact of plant control of nitrification on ecosystem functioning and dynamics depends on ecosystem properties that interact with N fluxes (e.g., nitrification rate, atmospheric deposition, leaching rates). This means that studying these impacts further is key to predicting where, in terms of soil properties, inputs of N or ecosystem types, inhibiting/stimulating plants should be more competitive. In the same vein, our results suggest that nitrification inhibition has the most potential for increasing plant biomass in systems when the baseline nitrification rate is high, which is the case in warm ecosystems (Li et al. 2019), and where atmospheric deposition is high.

Coexistence Mediated by the Control of Nitrification

While previous works illustrated how preference for various forms of N allows niche differentiation and promotes coexistence among species (Boudsocq et al. 2012; Konaré et al. 2019), our study shows how nitrification control acts as a second dimension for coexistence. In line with previous findings (Boudsocq et al. 2012; Konaré et al. 2019), we found that sufficient niche partitioning between the two forms of N allows coexistence. Our work highlights that nitrification control can also be construed as a niche construction process that modifies coexistence conditions. Priority effects occur when the niche construction effect is positive on the constructor species (e.g., an ammonium specialist inhibits nitrification) and negative on the other species (e.g., a nitrate specialist). On the other hand, when niche construction has a negative effect on the constructor (e.g., an ammonium specialist stimulates nitrification) and positive on the other species (e.g., a nitrate specialist), niche construction promotes coexistence (as in cross-feeding bacterial experiments; Turner et al. 1996). Graphical approaches usually used to describe coexistence conditions (Tilman 1980) and their extensions to niche-constructing phenotypes (Kylafis and Loreau 2011; Koffel et al. 2021) could not be used in this model because the two resources were not independent. Integrating nonindependent resources in a general theory of the niche opens up future research questions.

The Cost of Control of Nitrification

We hypothesized that nitrification control is energetically costly for the plant, and the cost is reflected by a decreased ability of plants to take up nutrients (see supplement F for the description of a costless scenario). Plants face a trade-off between investment in nitrification control and nutrient uptake. Empirically, the shape of that trade-off is completely unknown. Molecules excreted by inhibiting plants are small (Coskun et al. 2017), suggesting that the cost of producing an individual molecule is quite low. Nevertheless, the cost should also depend on the total amount of inhibiting molecules exuded, which has never been thoroughly documented (but see Sun et al. 2016). As expected, without a cost, stronger modulation rates are achievable by the plant population (i.e., no-extinction zone on the left and right in fig. H1; figs. D1, F1, G1, H1, H2 are available online). Maximal biomass is achieved for higher modulation rates relative to the case when there is a cost. Abrupt shifts between a lowly and highly productive state are also possible when control is not costly, but their extent depends on the maximum uptake rate (fig. H2). Since shapes of trade-offs may be strong determinants of eco-evolutionary dynamics (de Mazancourt and Dieckmann 2004), further empirical work should aim at establishing this cost function.

Perspectives

Our model could be further developed to take into account the spatial distribution of plants with various strategies toward nitrification and preferences for nitrate/ammonium and underlying mechanisms such as seed dispersal. While hydrophilic root exudates may diffuse in the soil and impact nitrification at the population scale (as was modeled in this study), hydrophobic root exudates are less mobile, and their effect may be restricted to the rhizosphere (Subbarao et al. 2007*b*; Coskun et al. 2017). Local nitrification control could generate heterogeneity in nutrient richness and modify interactions between neighboring plants. Previous works suggest that local facilitation may generate patchy vegetation patterns (Kéfi et al. 2007). Our proposed positive feedback could be used to investigate the spatial patchiness of grasses and trees in savannas, with grasses and trees likely having different strategies toward nitrification (Srikanthasamy et al. 2018).

BNI has been proposed as a means to increase fertilizer efficiency in agriculture (Lata et al. 2022). Because of high inputs of N, the nitrification rate in agricultural systems is high (Elrys et al. 2021), and inhibition of nitrification can increase productivity. Our results suggest that even plants having a strong preference for nitrate (which is the case of wheat) would have higher productivity if they were inhibiting nitrification. This supports and complements current arguments about the use of BNI to improve the efficiency of N fertilizers in agriculture and to decrease (1) the leaching of nitrate leading and related eutrophication issues in aquatic ecosystems and (2) denitrification highly contributing to global warming (Coskun et al. 2017; Subbarao and Searchinger 2021).

Conclusion

In this article, we investigated the ecological consequences of plant control of nitrification, the transformation of ammonium into nitrate. Since ammonium and nitrate are two forms of N available to plants, the control changes the condition of existence of a plant population, the productivity of the ecosystem, and coexistence conditions for different phenotypes. As with many niche-constructing activities, inhibiting nitrification opens an Allee niche (Koffel et al. 2021) for ammonium specialists, that is, increases the possibilities of existence of a plant population but undermines its resilience. At the community level (i.e., considering plants with different phenotypes), facilitation occurs when the controlling species increases the preferred form of N of the other species, which promotes coexistence. Our model highlights how the covariation of nitrification control and ammonium versus nitrate preference may largely change the functioning and stability of ecosystems, and we encourage the empirical characterization of such variation.

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Statement of Authorship

All authors conceived the model and contributed to the interpretation of results. A.N.A. performed the analysis and wrote the first draft. All authors made corrections and modifications and approved the submitted version.

Data and Code Availability

Scripts used to perform analysis and simulations and to produce figures 3–6 are available in Zenodo (https://doi.org/10.5281/zenodo.10151308; Ardichvili 2023).

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