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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 co-variation between plant control of nitrification and preference for ammonium vs. 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 (USA), 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 counter-intuitive (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.

# 1 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 (Diez et al., 2010; Klironomos, 2002; Reynolds et al., 2003). For example, soil and water retention by perennial species in semi-arid 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 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 due to litter transfer between patches of fixers and non-fixers (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., 2004, 1999, 2022; Srikanthasamy et al., 2021, 2022, 2018; Subbarao et al., 2009, 2007*a*). Crops such as sorghum, rice, maize, wheat and Bracharia exude molecules that block the enzymes involved in the first step of nitrification (Coskun et al., 2017; Subbarao et al., 2009; Zakir et al., 2008). 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 (He et al., 2022; Srikanthasamy et al., 2018). 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 towards ammonium. At the community level, available ammonium vs. 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 vs. nitrate and control of nitrification are likely to feed back on each other. Plants that inhibit nitrification will only benefit from this niche construction 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 vs. 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 (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 (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 (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 inter-specific effect should lead to priority effects and undermine coexistence (Tilman, 1980). To test these hypotheses, we compared all combinations of preference for nitrate vs. 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 4 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 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.

Figure 1 goes roughly here.

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

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

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

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

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

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 $l_D$ because of 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 $m_D$, 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 $\alpha$, and on plant biomass $P$

(equation 5, Fig. 2).

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

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 0. 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, $\beta_A$ and $\beta_N$, with $\beta_A + \beta_N = 1$. Ammonium uptake is $u\beta_A N_A$ and nitrate uptake $u\beta_N N_N$; note that when $\beta_A = \beta_N$ the proportion of ammonium (resp. nitrate) consumed by 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 ($\beta_A >> \beta_N$) while a nitrate specialist has a strong preference for nitrate ($\beta_N >> \beta_A$). 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 $\alpha$ (Fig. 2):

$$u(\alpha) = u_{max} e^{-\left(\frac{\alpha}{v}\right)^2} \tag{6}$$

$u$ 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.

Figure 2 goes roughly here.

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 (USA, 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 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/year (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 (though 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 0. 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 $\alpha$ and $\beta_A$ values, we numerically solve the differential equations to obtain all equilibrium values and their stability. We chose an interval for $\alpha$ 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 $\beta_A$ 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 suggest 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 $\alpha$ and $\beta_A$. With respect to question (ii), we study how the equilibrium plant biomass $P^*$ varies with $\alpha$ and $\beta_A$, expecting two local maxima in the $\alpha$ and $\beta_A$ 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 (equations 1-4 set to 0) to implicitly differentiate equilibrium compartments values with respect to $\alpha$. To address question (iii), i.e. 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 Online Supplement A). 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, coexistence is supposed maintained on the long term (Armstrong and McGehee, 1980).

All analyses (Ardichvili, 2023) are done using Wolfram Mathematica 12.2 (Wolfram Research Inc, 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 Online 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, $\alpha$, does not directly appear in equation 7. It only appears in the left-hand part of equation 7 in the uptake function $u(\alpha)$. Since $u(\alpha)$ is a decreasing function of $\alpha$, nitrification control only undermines the establishment of plants. Indeed, the strength of control depends on plant biomass, which is close to 0 at the moment of colonization. In small populations, plants only pay 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 on 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 + nitrate, yellow on Fig. 1, see Online 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 vs. 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 vs. nitrate on the resilience of a plant population already established. In some cases, the system can exhibit alternative stable states (e.g. Lamto parametrization on Fig. 3). In a range of $\alpha$ and $\beta_A$ values, the positive and the null equilibria are simultaneously stable. In that range of parameters, plant 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 plant density, which no longer retain ammonium to the point where insufficient resources cause the extinction of the plants.

Figure 3 goes roughly here.

Such bistability is present over a combination of nitrification control and preferences, and for different parametrizations (Fig. 4). With the Lamto parametrization, bistability is possible

for ammonium-consuming plants that inhibit nitrification (Fig. 4A). With Pawnee parameters, only restricted combinations of preference and control lead to alternative stable states (Fig. 4B). With the cultivated system parametrization, bistability occurs for many nitrification-inhibiting strategies, regardless of their preference (Fig. 4C). Finally, against our expectations, there is no bistability for the high nitrate parametrization (Fig. 4D). 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 (Online 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 which increases the area of bistability (Online 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 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 (Online Supplement H2).

We investigate how nitrification control and preference for ammonium vs. nitrate impact ecosystem productivity. Fig. 4 shows that plant biomass is affected in different ways by the four parametrizations. Consistent with Eq. 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, i.e. nitrification-inhibiting ammonium specialists with Lamto parameters (Fig. 4A) and nitrification-stimulating nitrate specialist with high nitrate parameters (Fig. 4D). 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. 4C), biomass production is maximal for a seemingly counter-intuitive 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. 4C). This implies that highly productive strategies may also be the least resilient.

Figure 4 goes roughly here.

## *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 0 (Online Supplement E), we obtained the following expression of how total N losses vary with control of nitrification:

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

$m_D/(l_D + m_D)d_P/(l_P + d_P) - 1$ 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 $\alpha$. In other words, inhibition of nitrification increases ecosystem productivity by minimizing total N losses. In Fig. 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 when (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 inter-specific effect should lead to priority effects and undermine coexistence. Fig. 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 parametrizations. Other $P_1$ strategies are investigated in Online Supplement F, as well as the cultivated and high nitrate parametrizations. Within a given panel of Fig. 5, coexistence by niche differentiation can be read along the vertical axis which corresponds to preference for ammonium of $P_2$. In panel C, for instance, drawing a vertical line through point a, coexistence is possible with species b1, an ammonium specialist, because its niche is sufficiently different from 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 panel C, species a can coexist with species b2 and not with species b3. Species b2 and b3 have similar preferences for nitrate, implying that niche differentiation is equally weak for the pairs of species a-b2 and a-b3. Species b2 however stimulates nitrification, which promotes the growth of the nitrate specialist species a, while species b3 inhibits nitrification, which suppresses the niche of species a. Coexistence is only possible for the facilitating interactor species b2. When species a is facilitated by species b2, its soil allows an increased availability of ammonium that favors species b2 and stable coexistence. In Fig. 5, Lamto and cultivated panels (A and C resp.) are more asymmetrical along the vertical axis than those of Pawnee and high nitrate (B and D resp.) A more complete observation of different $P_1$ strategies (cf. Online 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).

Figure 5 goes roughly here.

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 panels A and C). Online 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 vs. 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 4 parameter sets shows that external fluxes such as inputs or outputs determine which strategies lead to maximal productivity.

### *Nitrification control and ammonium vs. 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 on Fig. 1) on which the nitrate specialist relies (equation 7). Fig. 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.

Figure 6 goes roughly here.

Alternative stable states imply that the ecosystem may respond in an abrupt, unpredictable and non-linear 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 grassless, barren 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 only exist over a given range of combinations of inhibition and preference in our model, and the Lamto grasses may also be out of this range. A third hypothesis is that fire destroys only above-ground biomass, about 1/3 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 modelled 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, non-linear 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 (Boudsocq et al., 2011; Menge et al., 2012; Vitousek and Reiners, 1975).

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, due to the high leaching capacity of nitrate, no positive feedback leading to high productivity can exist for nitrification-stimulating nitrate specialist. In such systems, on the short term, stimulating nitrification may increase resource availability for a nitrate specialist but, on 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, Online 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 due to 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 further these impacts is key to predict 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 a 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 (Koffel et al., 2021; Kylafis and Loreau, 2011)could not be used in this model because the two resources were not independent. Integrating non-independent 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 Online 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 at the left and right in Fig. H1). 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 towards 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 (Coskun et al., 2017; Subbarao et al., 2007*b*). 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, grasses and trees likely having different strategies towards nitrification (Srikanthasamy et al., 2018).

Biological Nitrification Inhibition (BNI) has been proposed as a means to increase fertilizer efficiency in agriculture (Lata et al., 2022). Due to 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 a 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 paper, 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 many niche constructing activities, inhibiting nitrification opens an 'Allee niche' (Koffel et al., 2021) for ammonium specialists, i.e. 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 vs. nitrate preference may largely change the functioning and stability of ecosystems, and we encourage the empirical characterization of such variation.

## Acknowledgments

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## Statement of Authorship

All authors conceived the model and contributed to the interpretation of results. AA performed the analysis and wrote the first draft. All authors made corrections and modifications, and approve the submitted version.

## Data and code Accessibility

Scripts used to perform analysis, simulations, and produce Figures 3-6 are available online : https://zenodo.org/records/10151308

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# Tables

**Table 1: Variables, parameters, units, and default value**

| Symbol | Meaning | Unit | Pawnee[1] | Lamto[2] | 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$^{-1}$ | 0.258 | 0.6 | 0.6 | 0.6 |
| $l_P$ | plant loss rate | yr$^{-1}$ | 0 | 0.4 | 0.4 | 0.4 |
| $R_D$ | annual inputs of detritus | kg ha$^{-1}$ yr$^{-1}$ | 0 | 16 | 16 | 16 |
| $m_D$ | mineralization rate | yr$^{-1}$ | 0.01338 | 0.025 | 0.025 | 0.025 |
| $l_D$ | detritus loss rate | yr$^{-1}$ | 0.01338 | 0.0027 | 0.0027 | 0.0027 |
| $u_{max}$ | maximum uptake rate | yr$^{-1}$ | 0.136 | 0.14186 | 0.14186 | 0.14186 |
| $R_A$ | annual inputs of ammonium | kg ha$^{-1}$ yr$^{-1}$ | 3 | 23 | 50 | 4.1 |
| $l_A$ | ammonium loss rate | yr$^{-1}$ | 0.05 | 0.0133 | 0.0133 | 2.7 |
| $R_N$ | annual inputs of nitrate | kg ha$^{-1}$ yr$^{-1}$ | 3 | 4.1 | 50 | 23 |
| $l_N$ | nitrate loss rate | yr$^{-1}$ | 0.15 | 2.7 | 2.7 | 0.0133 |
| $n_0$ | nitrification rate in the absence of plants | yr$^{-1}$ | 0.05 | 2.7 | 5 | 2.7 |
| $n_{max}$ | maximum nitrification rate | yr$^{-1}$ | 0.1 | 4.16 | 10 | 27 |
| $\alpha$ | strength of control of nitrification | kg$^{-1}$ ha | - | - | - | - |
| $v$ | cost of nitrification control | kg$^{-1}$ ha | 0.5* | 0.05* | 0.05* | 0.05* |
| $\beta_A$ | plant preference for ammonium | - | - | - | - | - |
| $\beta_N$ | plant preference for nitrate | - | - | - | - | - |

[1] from Woodmansee et al., 1978
[2] from Boudsocq et al., 2009
* Except $v$ which has not been estimated in the ecosystems. For a discussion on the value of $v$, see Online Supplement H.

# Figure legends

**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 Eq. 7 are illustrated with thick arrows. Orange: first recycling loop – N only travels through the detritus ($D$), ammonium ($N_A$), and plant ($P$) compartments. Yellow: second recycling loop - N travels through both the ammonium ($N_A$) and nitrate ($N_N$) compartments in addition to the plant ($P$) and detritus ($D$) compartments.**

**Figure 2: A. Nitrification rate as a function of plant biomass, for different levels of control ($\alpha$ values in (-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 $v = 0.05$**

**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 $\alpha$, 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 $\alpha$ 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).**

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

**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 and C) and Pawnee (B and D) parametrizations. A-B: $P_1$ is an inhibiting ammonium specialist; C-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 b1 on panel 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 b2 and b3 on panel C).**

**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, which decreases N losses, creating a positive feedback loop. On the contrary, Pawnee plants do not have much room for modifying the nitrification rate; the impact of inhibition in Pawnee is minor (D). A: $\alpha = 0$; $\beta_A = \beta_{A_{opt}} = 0.6$. B: $\alpha = 0$; $\beta_A = \beta_{A_{opt}} = 0.63$. C: $\alpha = \alpha_{opt} = -0.049$; $\beta_A = \beta_{A_{opt}} = 0.6$. D: $\alpha = \alpha_{opt} = -0.005$; $\beta_A = \beta_{A_{opt}} = 0.63$**

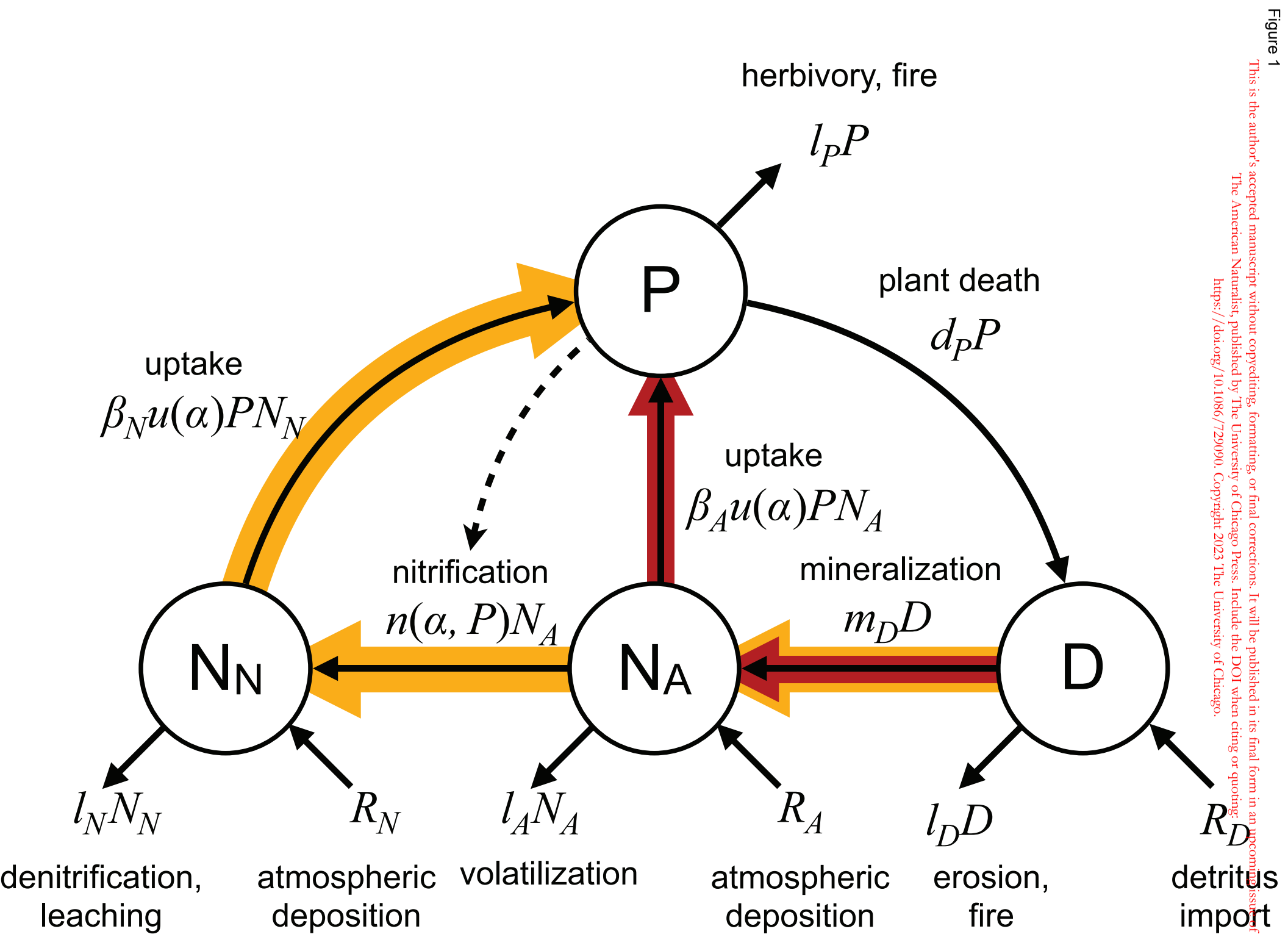
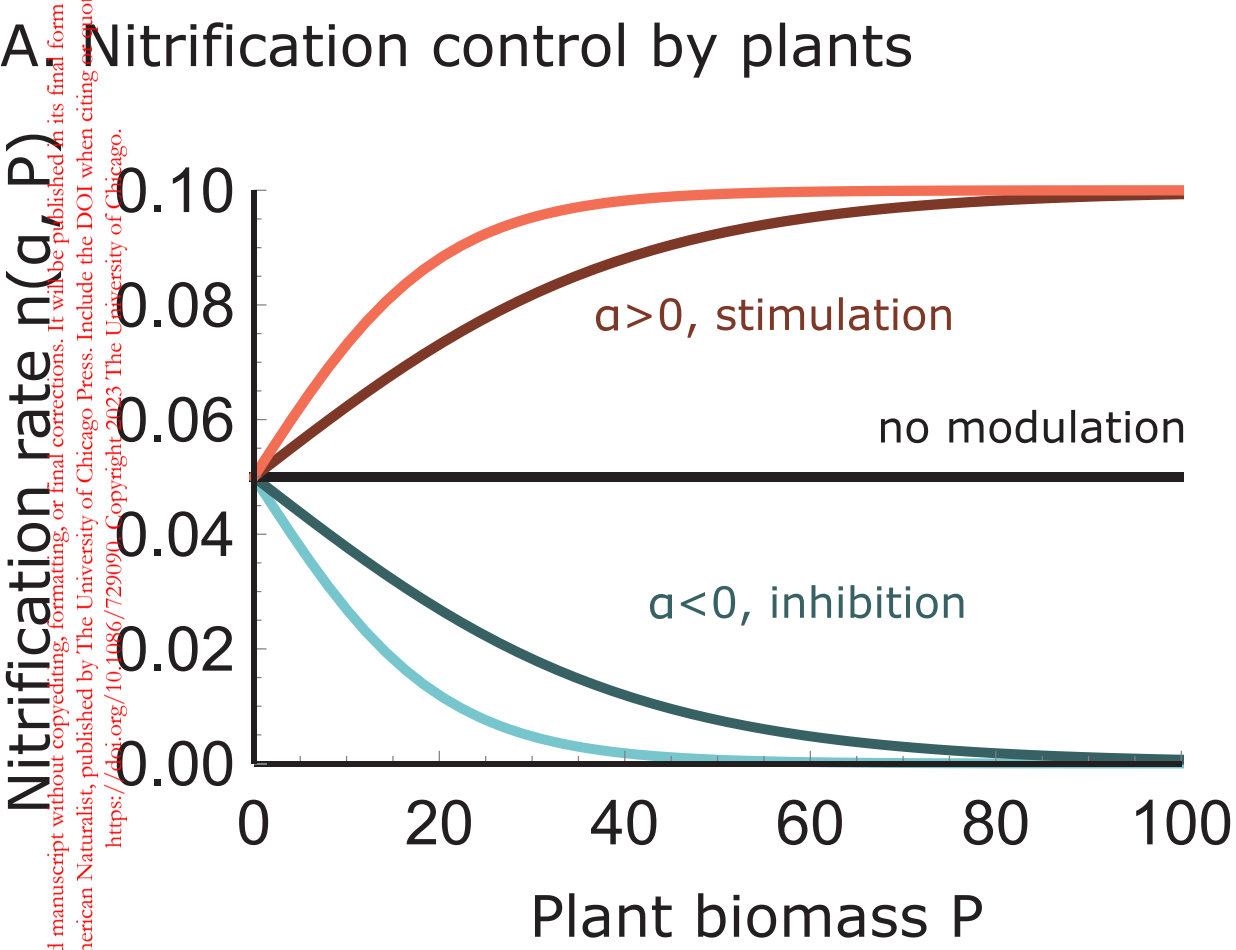



Figure 1



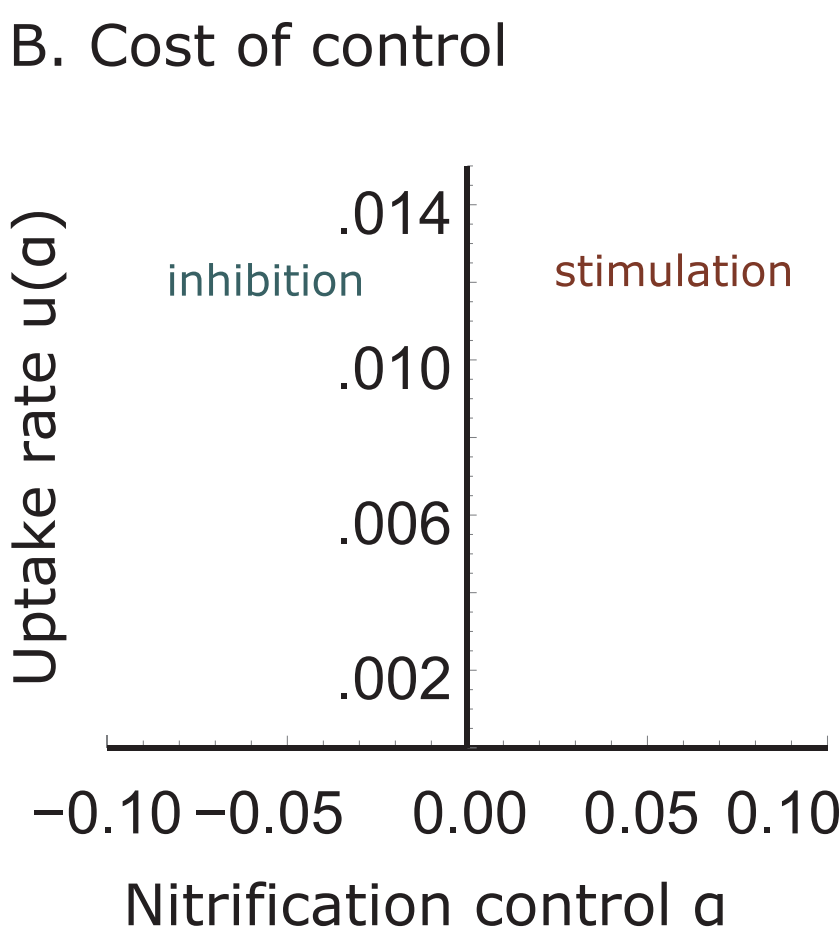




Figure 2

Figure 3



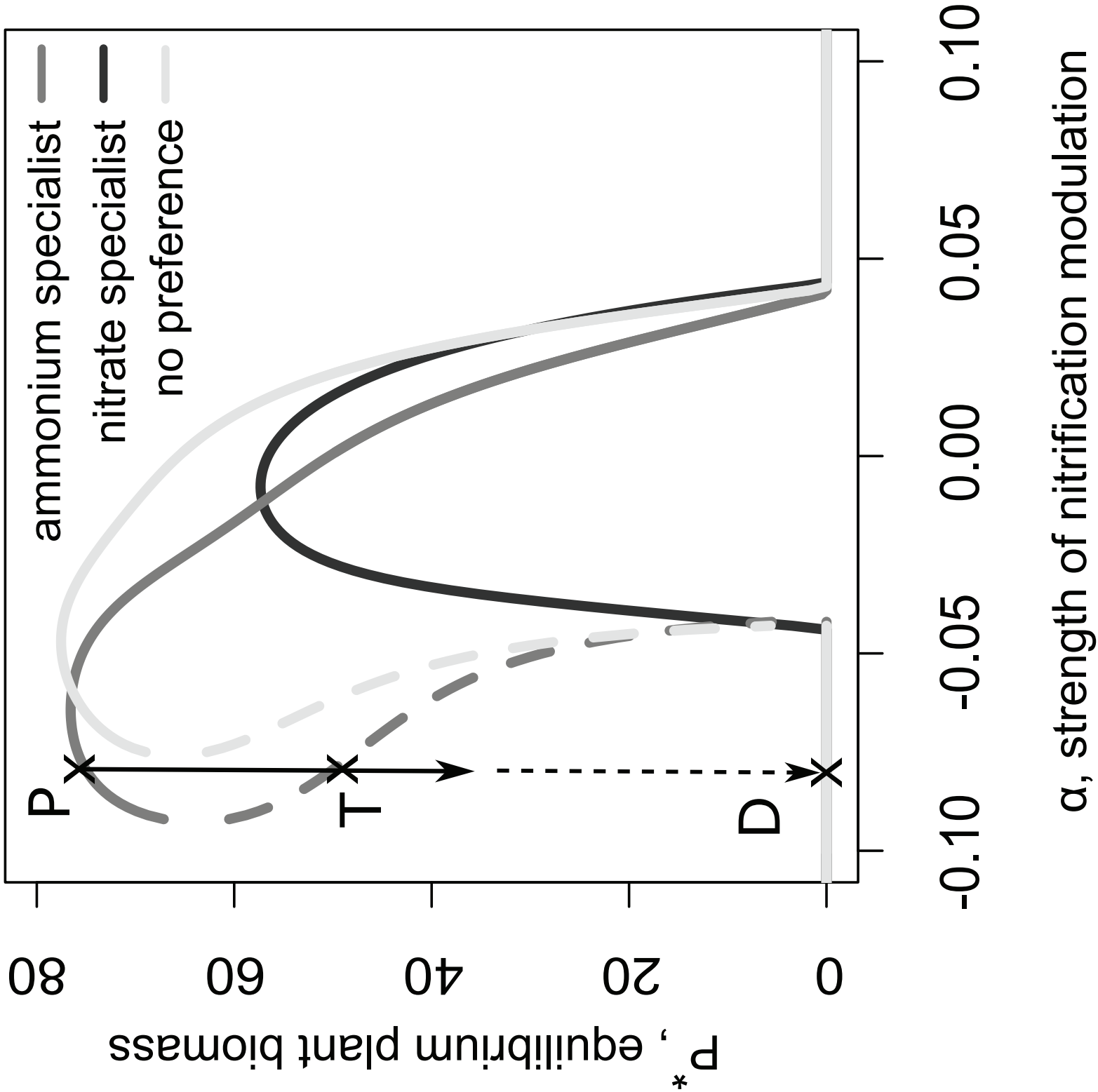


Figure 4



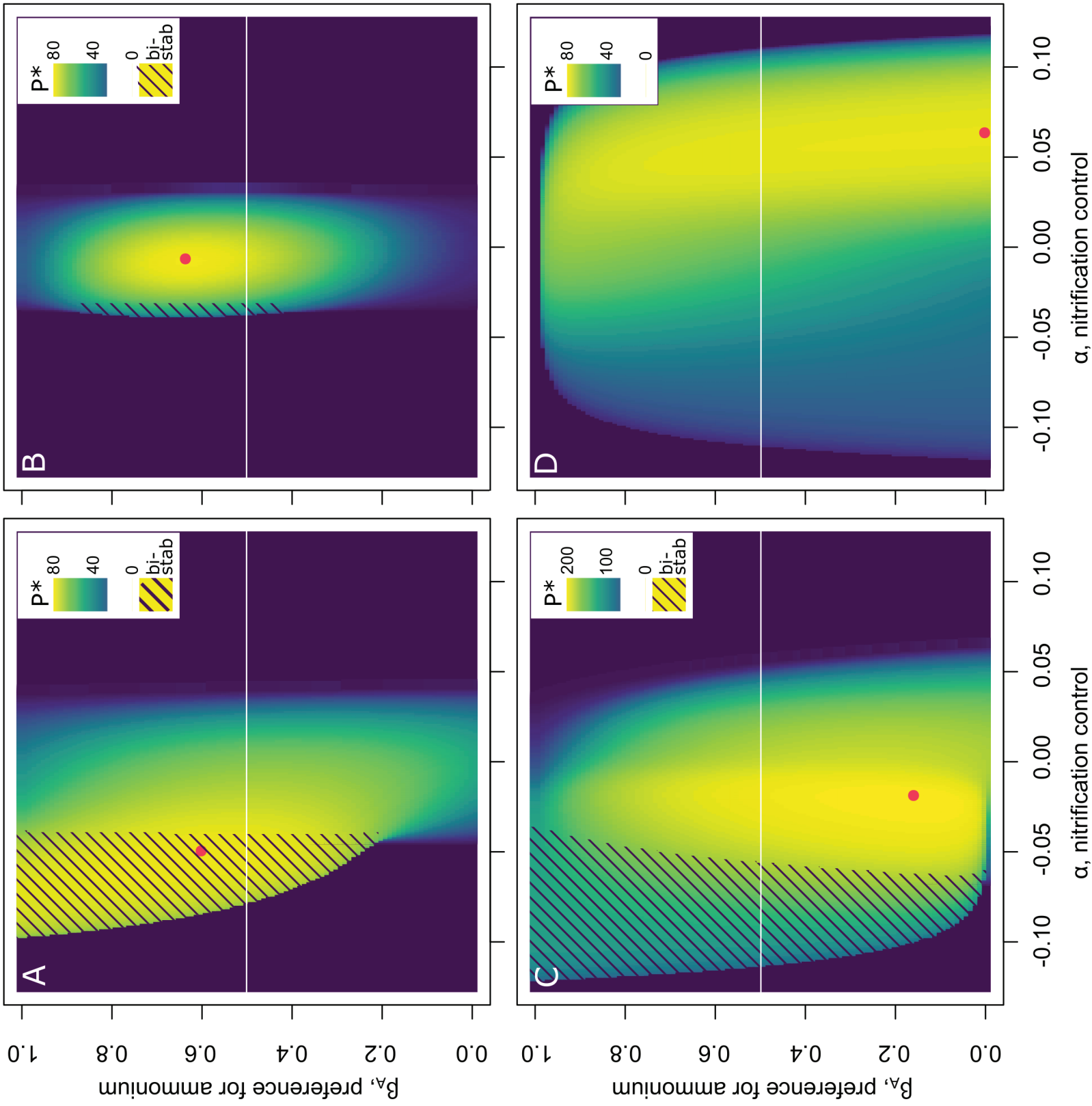
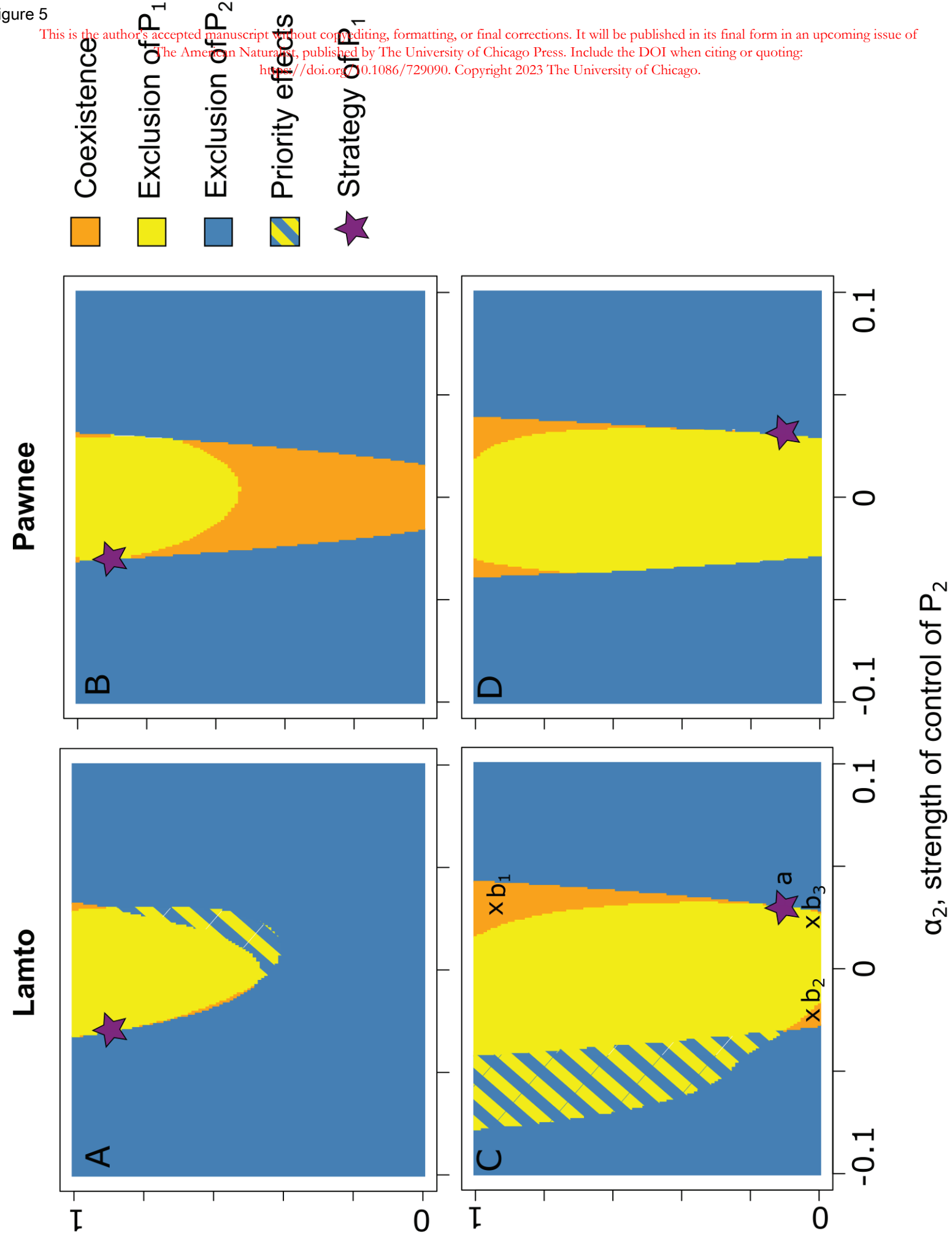


Figure 5

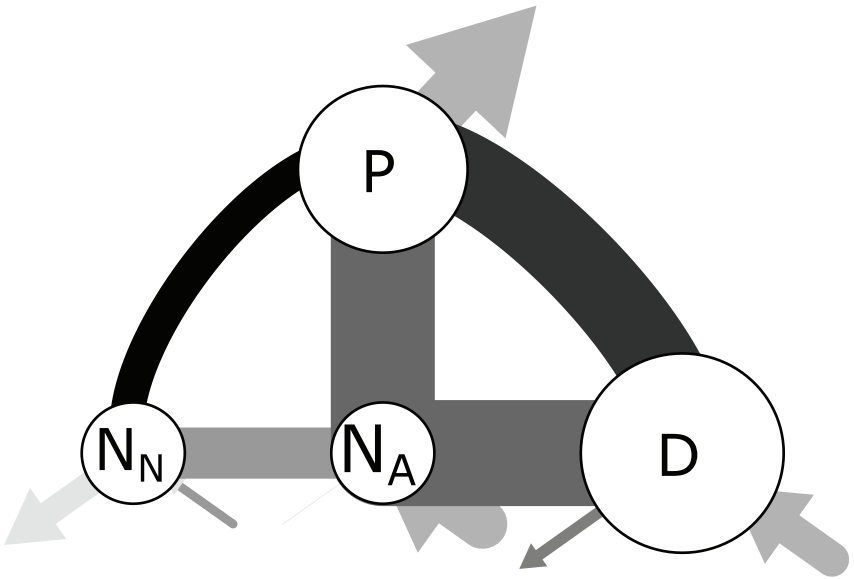




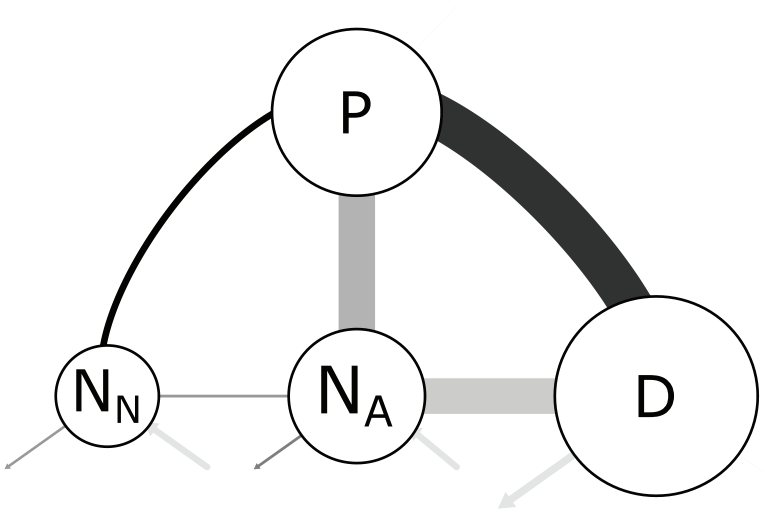
Lamto

Pawnee

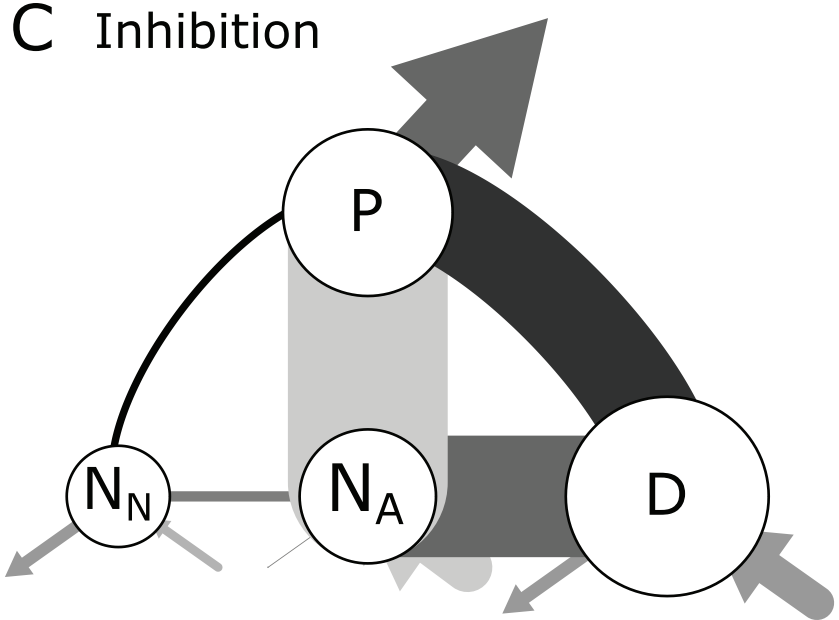
A No control




B No control




C Inhibition




D Inhibition

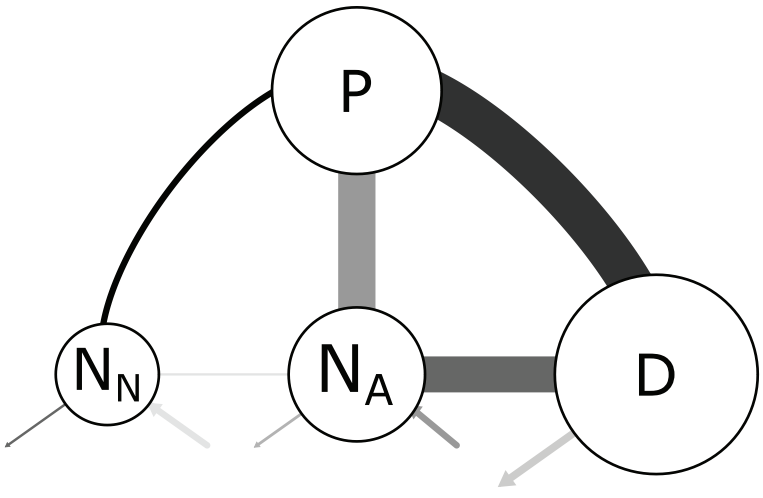



Figure 6

This is the author's accepted manuscript without copyediting, formatting, or final corrections. It will be published in its final form in an upcoming issue of The American Naturalist, published by The University of Chicago Press. Include the DOI when citing or quoting: https://doi.org/10.1086/729090. 

# Online Supplement:

# Nitrification control by plants and preference for ammonium vs. nitrate: positive feedbacks increase productivity but undermine resilience

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# Supplement A: Mutual invasions in a two-plant system

The dynamics of N in a two-plant system are described by the following equations:

$$\frac{dP_1}{dt} = \left(u(\alpha_1)\beta_{A1}N_A + u(\alpha_1)\beta_{N1}N_N - d_P - l_P\right)P_1 \tag{A1}$$

$$\frac{dP_2}{dt} = \left(u(\alpha_2)\beta_{A2}N_A + u(\alpha_1)\beta_{N2}N_N - d_P - l_P\right)P_2 \tag{A2}$$

$$\frac{dD}{dt} = R_D + d_P(P_1 + P_2) - (m_D + l_D)D \tag{A3}$$

$$\frac{dN_A}{dt} = R_A + m_D D - (u(\alpha_1)\beta_{A1}P_1 + u(\alpha_2)\beta_{A2}P_2)N_A - n(\alpha_1, P_1, \alpha_2, P_2)N_A - l_A N_A \tag{A4}$$

$$\frac{dN_N}{dt} = R_N + n(\alpha, P)N_A - (u(\alpha_1)\beta_{N1}P_1 + u(\alpha_2)\beta_{N2}P_2)N_N - l_N N_N \tag{A5}$$

with

$$n(\alpha_1, P_1, \alpha_2, P_2) = n_{max}\frac{e^{\alpha_1 P_1 + \alpha_2 P_2}}{e^{\alpha_1 P_1 + \alpha_2 P_2} - 1 + \frac{n_m ax}{n_0}} \tag{A6}$$

We evaluate:

$$\frac{1}{P_1}\frac{dP_1}{dt}\Big|_{P_1=0, P_2=P_2^*} \tag{A7}$$

and

$$\frac{1}{P_2}\frac{dP_2}{dt}\Big|_{P_1=P_1^*, P_2=0} \tag{A8}$$

The issue of the mutual invasions is then classified according to the sign of these two expressions:

- A7 $> 0$ & A8 $> 0$ $\rightarrow$ Coexistence is possible
- A7 $< 0$ & A8 $< 0$ $\rightarrow$ Priority effects
- A7 $> 0$ & A8 $< 0$ $\rightarrow$ $P_1$ excludes $P_2$
- A7 $< 0$ & A8 $> 0$ $\rightarrow$ $P_2$ excludes $P_1$

# Supplement B: Equilibrium soil N content without plants

In the absence of plants, detritus N content, soil ammonium and soil nitrate reach the following equilibrium values:

$$\begin{aligned} D_0^* &= \frac{R_D}{l_D + m_D} \\ N_{A0}^* &= \frac{1}{l_A + n_0}\left(R_A + \frac{m_D R_D}{l_D + m_D}\right) \\ N_{N0}^* &= \frac{1}{l_N}\left(R_N + \frac{n_0}{l_A + n_0}\left(R_A + \frac{m_D R_D}{l_D + m_D}\right)\right) \end{aligned} \tag{B1}$$

In fact, the invasibility condition can be rewritten:

$$u(\alpha) > \frac{d_P + l_P}{\beta_A N_{A0}^* + \beta_N N_{N0}^*} \tag{B2}$$

## Supplement C: Total N recycling is the sum of two different loops

In this section, we detail the recycling loops appearing in Eq. 7 and are presented in Fig. 1. Considering an ammonium specialist, Eq. 7 becomes:

$$u(\alpha) > \frac{d_P + l_P}{\beta_A \left( \frac{1}{l_A + n_0} \left( R_A + \frac{m_D R_D}{l_D + m_D} \right) \right)} \tag{C1}$$

In the denominator, $R_A$ is the rate of inputs in the ammonium compartment while $l_A$ and $n_0$ are two rates of losses (nitrification is a loss to the system for an ammonium specialist), therefore $\frac{1}{l_A+n_0} R_A$ represents the quantity of ammonium (in kg ha$^{-1}$) that is available for plant to take up directly from the ammonium compartment. Yet, ammonium specialists also have another source of soil N: detritus inputs that have been mineralized. Similarly, $\frac{1}{l_A+n_0} R_D$ is a quantity (kg ha$^{-1}$) which is scaled by the internal recycling efficiency of the detritus compartment ($\frac{m_D}{m_D+l_D}$, ie. the fraction of N that stays in the system after traveling in the D compartment - dimensionless), so that $\frac{1}{l_A+n_0} \frac{m_D}{m_D+l_D} R_D$ represents the quantity of N that enters the system as detritus input and can be taken up as ammonium by plants.

Considering a nitrate specialist, Eq. 7 becomes:

$$u(\alpha) > \frac{d_P + l_P}{\beta_N \left( \frac{1}{l_N} \left( R_N + \frac{n_0}{l_A + n_0} \left( R_A + \frac{m_D R_D}{l_D + m_D} \right) \right) \right)} \tag{C2}$$

This time, $R_N$ is the rate of inputs in the nitrate compartment, while $l_N$ is the only possible loss rate from this compartment. $\frac{1}{l_N} R_N$ corresponds to the quantity of N (kg ha$^{-1}$) that can be taken up directly from the nitrate compartment. $\frac{1}{l_N} R_A$ is also a quantity of N (kg ha$^{-1}$) that is scaled by the internal recycling efficiency of the ammonium compartment $\frac{n_0}{l_A+n_0}$ so that $\frac{1}{l_N} \frac{n_0}{l_A+n_0} R_A$ corresponds to the N quantity that enters the system as ammonium and can be absorbed by plants as nitrate. Finally, $\frac{1}{l_N} R_D$ (kg ha$^{-1}$) is scaled by the recycling efficiency of both the ammonium compartment $\frac{n_0}{l_A+n_0}$ and the detritus compartment $\frac{m_D}{m_D+l_D}$, implying that $\frac{1}{l_N} \frac{n_0}{l_A+n_0} \frac{m_D}{m_D+l_D} R_D$ is the N quantity that enters the system as detritus, but can be absorbed as nitrate by plants.

## Supplement D: Elasticity analysis of bistability to all parameters

For each parameter, in each ecosystem we computed the equilibrium values of each compartment and their stability by applying a 10% increase and a 10% decrease in the parameter. In Fig. B1, the relative change in the number of bi-stable pixels to an increase or decrease is displayed. For example, a 10% increase in parameter $d_P$ leads to 7% decrease in the area of bistability in Lamto, and to a 4% decrease in the area of bistability in Pawnee.

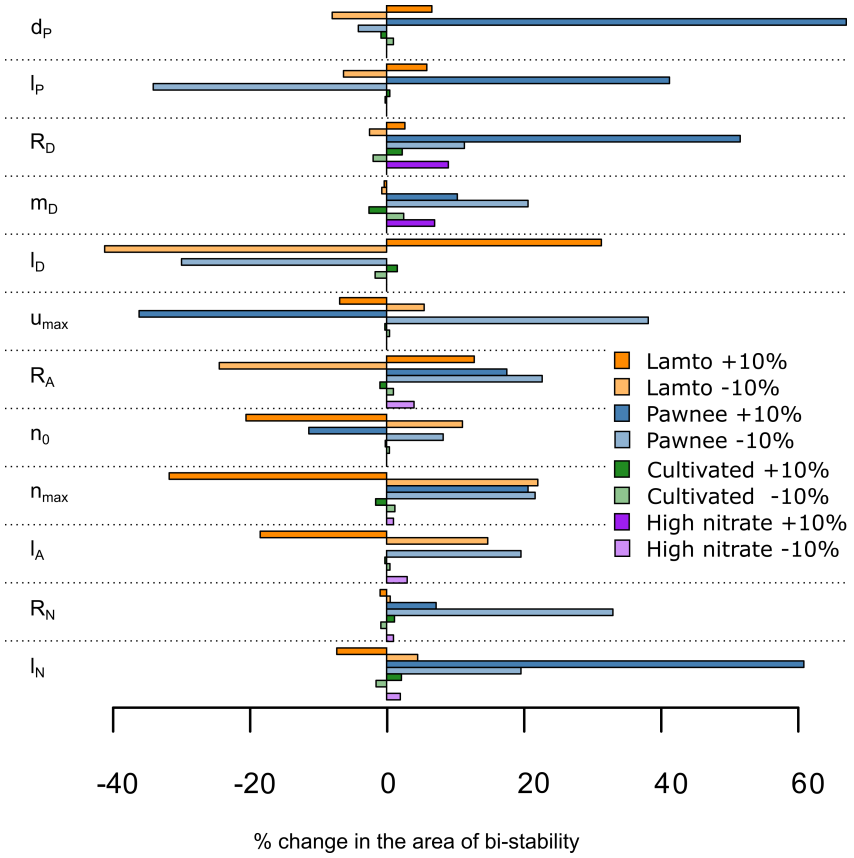


Figure D1: % change in the area of bistability $A$ with an increase or decrease in each parameter $p$ (computed as $\frac{\Delta A/A}{\Delta p/p}$). For the high-nitrate model in which there are no bi-stable pixels, the number of bi-stable pixels is shown.

Longer bars imply that the area of bistability is sensitive to the parameter. The diversity of responses suggests that there is not a single parameter that drives potential bistability. With the

Lamto and Pawnee parametrizations, the area of bistability is quite sensitive to the parameter $l_P$ , $d_P$, $l_D$. An increase in plant loss rate, mortality or organic matter loss rate decreases the area of bistability, since those fluxes draw energy out of the positive feedback. The effect of a perturbation in $u_{max}$, $R_A$, $n_0$, $l_A$, $R_N$ and $l_N$ is counter-intuitive in Pawnee. Indeed, either an increase or decrease in the parameter increases the area of bistability. This is mainly because these parameters alter the shape of the area of bistability, and the resulting change in area is just a result of this shape change and may not reflect any directionality in the effect of that parameter on the resilience of the system. With the high-nitrate parameter set, the area of bistability clearly depends on inputs and losses of ammonium and nitrate ($R_A$ and $R_N$, $l_A$ and $l_N$), suggesting that these parameters are key in fueling the positive feedback described in the main text.

# Supplement E: Plant productivity is maximal when N losses are minimal

In this section, we study how equilibrium compartment values change with nitrification control. We assume that a positive and stable equilibrium exists and use equilibrium conditions to make simplifications. For example, to study the variations of detritus equilibrium value with respect to nitrification control, assuming that the compartment is at equilibrium allows to set:

$$(2) = 0 \tag{E1}$$

$$R_D + P^* d_P - D^*(m_D + l_D) = 0 \tag{E2}$$

Since we do not have the expressions of compartments values, we assume that they vary with $\alpha$, and use their implicit differentiation with respect to $\alpha$ to continue calculations. Conversely, the input parameter $R_D$ does not vary with $\alpha$.

$$\frac{\partial \left(R_D + d_P P^* - (m_D + l_D) D^*\right)}{\partial \alpha} = 0 \tag{E3}$$

$$d_P \frac{\partial P^*}{\partial \alpha} - (m_D + l_D) \frac{\partial D^*}{\partial \alpha} = 0 \tag{E4}$$

$$\frac{\partial D^*}{\partial \alpha} = \frac{d_P}{m_D + l_D} \frac{\partial P^*}{\partial \alpha} \tag{E5}$$

$$\tag{E6}$$

Eq. D4 means that the detritus compartment and the plant compartment have the same variations with respect to $\alpha$. Indeed, since $\frac{d_P}{m_D + l_D}$ is positive, when $\frac{\partial D^*}{\partial \alpha}$ is positive, so is $\frac{\partial P^*}{\partial \alpha}$. When the detritus compartment increases with nitrification control, so does the plant compartment.

Using the equilibrium conditions of the other compartments results in setting $\frac{\partial P^*}{\partial t} = 0$ and $\frac{\partial {N_A}^*}{\partial t} = 0$ and $\frac{\partial {N_N}^*}{\partial t} = 0$, which enables to write:

$$(1) + (3) + (4) = 0 \tag{E7}$$

$$-(l_P + d_P)P^* + m_D D^* + R_{N_A} - l_{N_A} {N_A}^* + R_{N_N} - l_{N_N} {N_N}^* = 0 \tag{E8}$$

We compute the partial derivative:

$$\frac{\partial \left(-(l_P + d_P)P^* + m_D D^* + R_{N_A} - l_{N_A} {N_A}^* + R_{N_N} - l_{N_N} {N_N}^*\right)}{\partial \alpha} = 0 \tag{E9}$$

$$-\frac{\partial P^*}{\partial \alpha}(l_P + d_P) + \frac{\partial D^*}{\partial \alpha} m_D - \frac{\partial {N_A}^*}{\partial \alpha} l_{N_A} - \frac{\partial {N_N}^*}{\partial \alpha} l_{N_N} = 0 \tag{E10}$$

Subbing in Eq. D1, we obtain the result of Eq. 8:

$$-\frac{\partial P^*}{\partial \alpha}(l_P + d_P) + \frac{\partial D^*}{\partial \alpha}\frac{m_D d_P}{m_D + l_D} - \frac{\partial {N_A}^*}{\partial \alpha} l_{N_A} - \frac{\partial {N_N}^*}{\partial \alpha} l_{N_N} = 0 \tag{E11}$$

$$\frac{\partial P^*}{\partial \alpha}\left(\frac{m_D d_P}{m_D + l_D} - l_P - d_P\right) = \frac{\partial {N_A}^*}{\partial \alpha} l_{N_A} + \frac{\partial {N_N}^*}{\partial \alpha} l_{N_N} \tag{E12}$$

$$\frac{\partial P^*}{\partial \alpha}\left(\frac{m_D}{m_D + l_D}\frac{d_P}{d_P + l_P} - 1\right)(d_P + l_P) = \frac{\partial \left({N_A}^* l_{N_A} + {N_N}^* l_{N_N}\right)}{\partial \alpha} \tag{E13}$$

# Supplement F: Coexistence conditions depend on nitrification control strategies

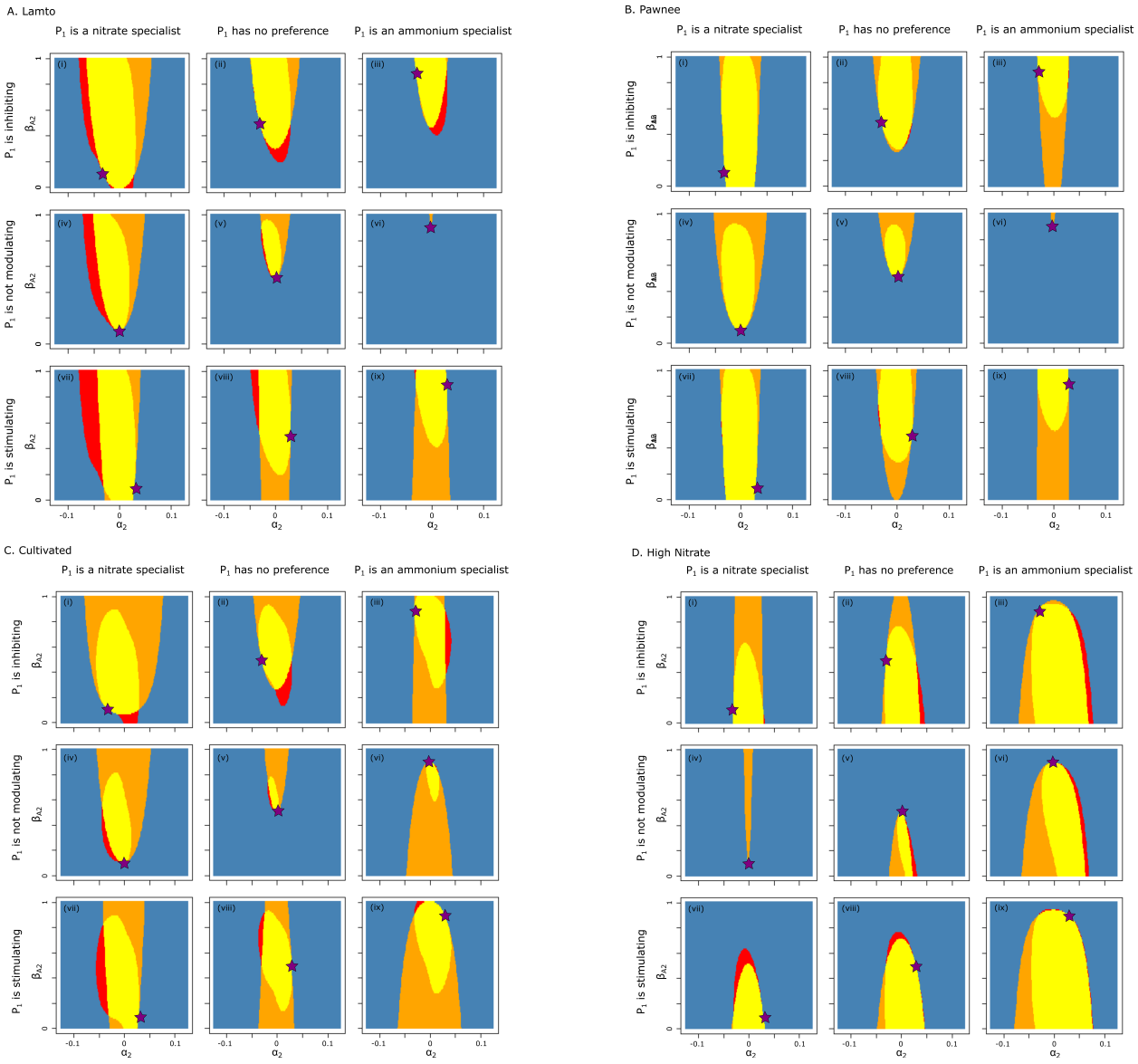


Figure F1: Results of the mutual invasions for 9 fixed strategies of plant A against a range of strategies $(\alpha_B, \beta_{1B})$ of plant B. Orange: strategies coexist; blue: A excludes B; yellow: B excludes A; red: priority effect.

We stress that in such panels, whenever coexistence is possible for species that are opposed on the vertical axis, coexistence is explained by niche differentiation. In addition, variations in nitrification control can lead to niche construction, whose effect can be read from the asymmetry between the left and right halves of the panel.

By focusing on the effect of the fixed strategy, we notice several things: for every parameter set, contrary to our expectations, the strategies creating their own niches (panels i and ix) are not the most competitive strategies. Compared to other panels, panels i and ix are not the panels with the largest blue region.

However, among plants that do not have a preference (along a horizontal line across the star in panel ii, v, viii), nitrification control does not promote coexistence since coexistence requires niche differentiation to some degree.

With Lamto and cultivated ecosystems, coexistence is mediated by the combination of niche differentiation and facilitation by niche construction. For example, in panel i and iv, a nitrate specialist can coexist with an ammonium specialist (niche differentiation) or a plant that has no preference but creates a favorable environment for the other species by stimulating nitrification (facilitation). It is also the case for plants that do not have any preference (ii and v) that can coexist with ammonium specialists stimulating nitrification. Symmetrically, ammonium specialists stimulating nitrification (panel ix) can coexist with nitrate specialists or plants that do not have a preference.

With Pawnee parameters, the direction of control (stimulation vs. inhibition) has small effects: panels i, ii, iii, vii, viii, ix are all relatively symmetrical, and symmetrical to each other (i-vii, ii-viii, iii-ix), implying that niche construction by nitrification control does not alter coexistence outcomes. The cost of control seems to outweigh the associated benefits, which may be explained by the fact that nitrification with Pawnee parameters is not allowed to reach high values (Table 1). However, niche differentiation seems to explain coexistence patterns: in i, iv, vii, nitrate specialists can coexist with ammonium specialists; in iii, vi, ix, ammonium specialists can coexist with nitrate specialists.

# Supplement G: Elasticity analysis of strategies that enable maximal productivity $(\alpha_{max}, \beta_{A_{max}})$ to all parameters

In this section, we identify which parameters most influence the most productive strategies. In all parametrizations, the baseline nitrification rate and maximum nitrification have an important impact on the position of maximal productivity. An increase in the baseline nitrification increases the potential effect of inhibition of nitrification, and the optimal strategies move towards more inhibition and higher preference for ammonium.

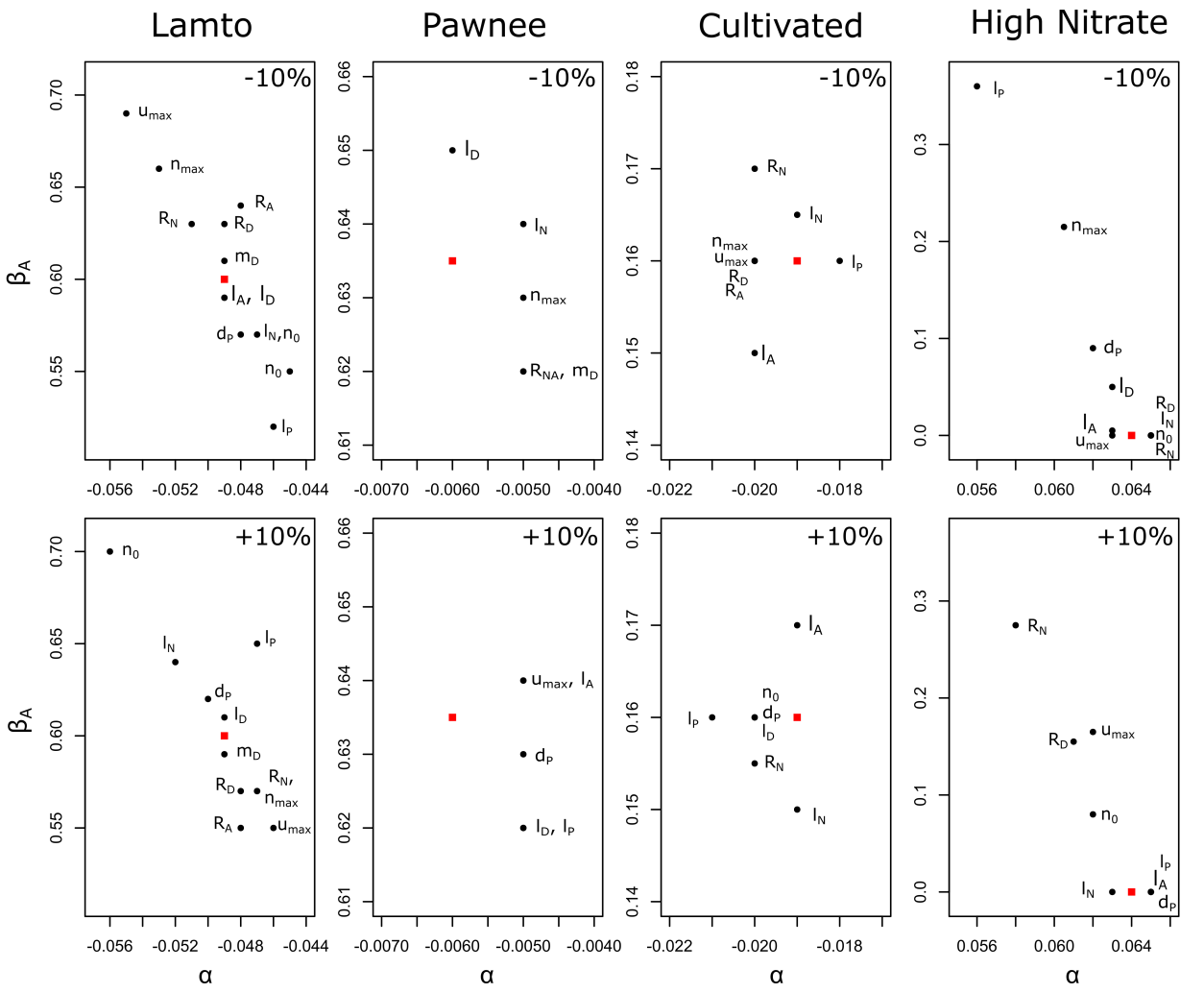


Figure G1: Response of the combination of nitrification control and plant preference for ammonium that enables maximal productivity to a 10% increase and decrease in each parameter. The red square is the combination that allows maximal productivity for default parameters. Parameters that do not appear do not influence the position of maximal productivity.

# Supplement H: Ecological consequences of costless control of nitrification and preference for ammonium vs. nitrate

Removing the cost of nitrification does not yield the expected two local maxima in plant productivity (Fig. H1). However, in all systems, maximum biomass production occurs for maximal control (inhibition for Lamto, Pawnee and cultivated sets, stimulation for the high-nitrate parametrization). The patterns are quite different with each set of parameters, suggesting that nitrification control drives ecosystem productivity in Lamto, the cultivated field and the high nitrate parametrization (more variation along the horizontal axis than along the vertical axis) while preference for ammonium vs. nitrate does in Pawnee.

With that set of parameters, removing the cost completely removes the possibilities of bistability, as expected from Eq. 7. However, the positive feedback responsible for alternative stable states is still present. In fact, by sufficiently decreasing the maximum uptake rate $u_{max}$, the null equilibrium becomes stable again and alternative stables states are possible.

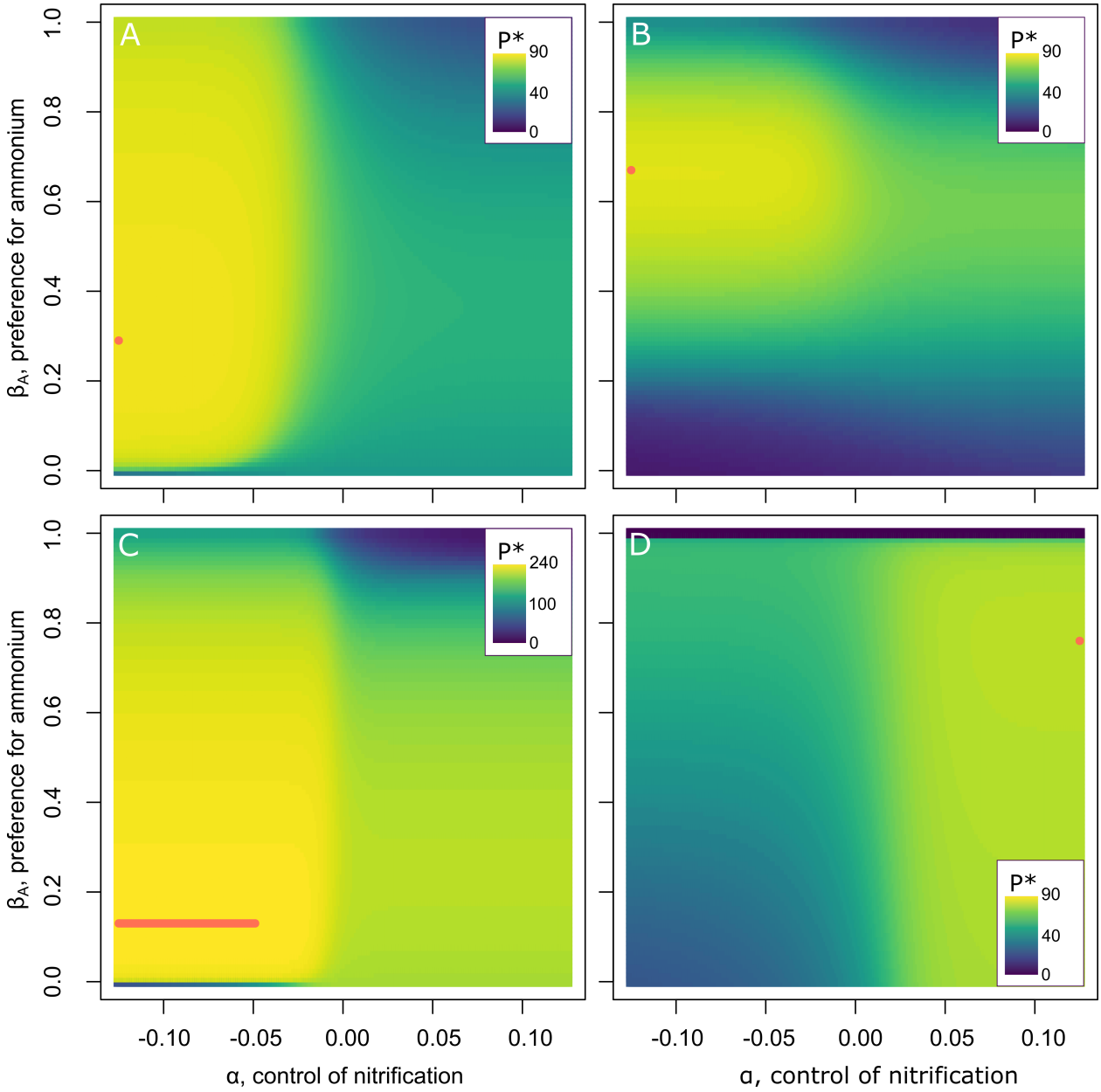


Figure H1: Equilibrium plant biomass ($P^*$) as a function of nitrification control and preference for ammonium vs. nitrate with Lamto (A), Pawnee (B), cultivated (C) and high nitrate (D) parameters.

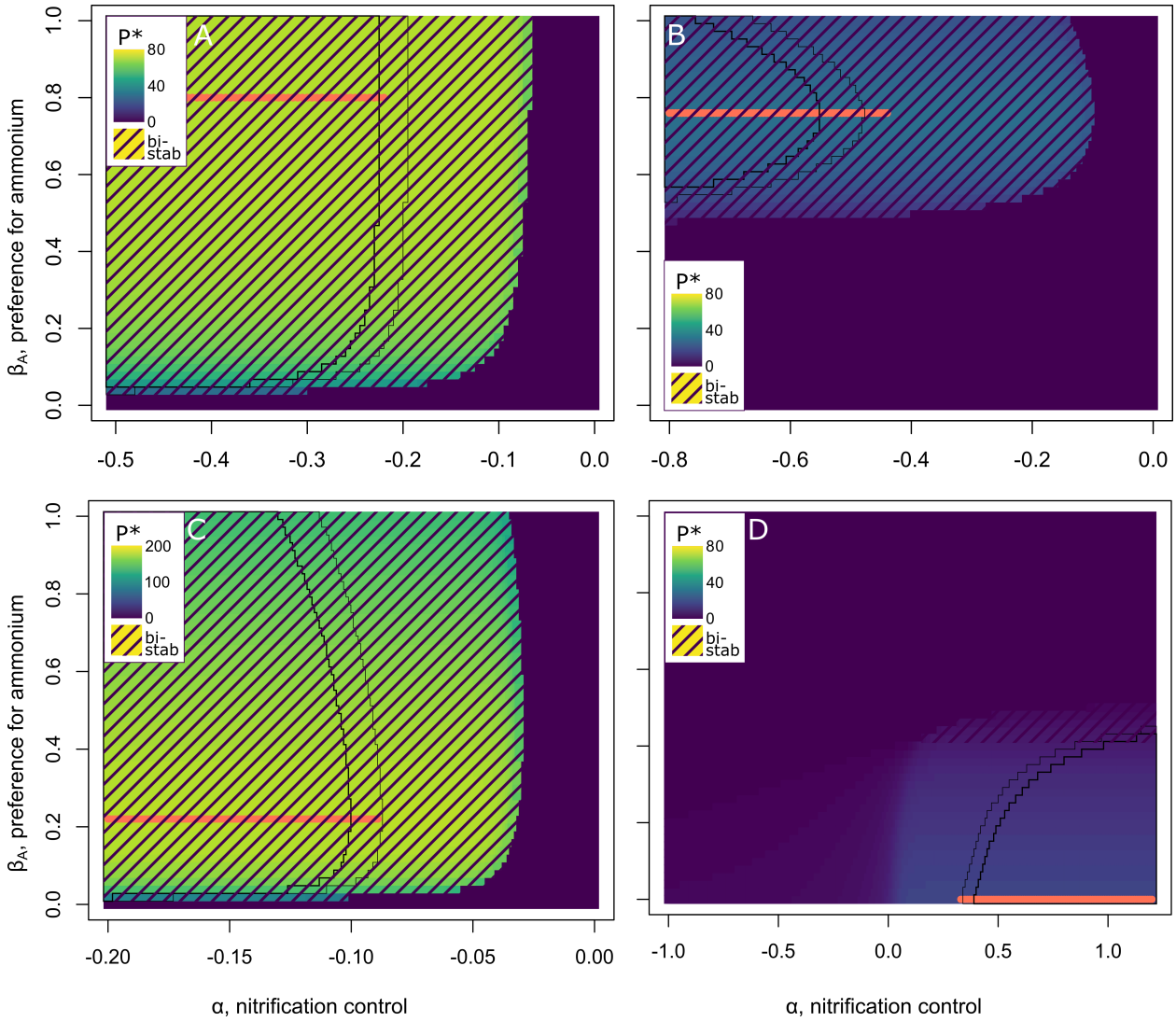


Figure H2: Equilibrium plant biomass ($P^*$) as a function of nitrification control and preference for ammonium vs. nitrate when control is costless with A. Lamto parameters, but $u_{max} = 0.014186 = u_{max-Lamto} \cdot 0.10$, B. Pawnee parameters, but $u_{max} = 0.00668 = u_{max-Pawnee} \cdot 0.5$, C. cultivated, but $u_{max} = 0.014186 = u_{max-cultivated} \cdot 0.10$ and D high nitrate parameters, but $u_{max} = 0.0007093 = u_{max-hn} \cdot 0.005$. The red line is where maximal plant biomass is achieved. The thin black line delineates the region where the nitrification rate is less than $10^{-6}$ in A, B, C ; and more than $n_{max} - 10^{-6}$ in D. The thicker black line delineates the region where the nitrification rate is less than $10^{-7}$ in A, B, C ; and more than $n_{max} - 10^{-7}$ in D. In those regions, equilibrium values do not change with $\alpha$ since the nitrification rate has reached its limit. The equilibrium is thus feasible for smaller values of $\alpha$ in A, B, C and larger values in D.