A Continuous Model of Nutrient Dynamics and N Fixation

Daniel Bauman

April 18, 2023

Abstract

We create a continuous partial-differential-integral equation modeling nutrient transfer in a forest. Nitrogen and Phosphorus cycle between plants, leaf litter, soil organic matter and plant-available nutrients. We compare the growth rates of nitrogen-fixing plants versus plants which do not fix nitrogen in a spatial region, and evaluate how parameters including the rooting radius, litterfall distribution, and advection and diffusion of litter change these competitive dynamics. We find that Nitrogen fixation is most advantageous when plants have root overlap, significant turnover occurs, and there is no spatial movement of litter through advection and diffusion. Meanwhile, Nitrogen fixers perform the worst compared to non-fixers when the maximum rooting radius is small and litterfall occurs farther beyond the trees. The competitive balance also shifts over time, with fixers almost always doing better in the first 10-20 years of the model, while usually performing poorly afterwards. This reflects that they induce an environment that is more favorable to their competitors, and highlights the need to understand how Nitrogen fixation can be maintained in Nitrogen-rich forests.

1 Introduction

Nitrogen is a crucial element for all forms of organic life. However, although it is the most abundant element in the earth's atmosphere, it is seldom in a form which can be used by organisms. Plants require nitrogen to grow, and it is often a limiting nutrient in terrestrial ecosystems [BM21]. Nitrogen fixation is the process by which microbes convert nitrogen into plant-usable compounds. Although free-living microbes fix nitrogen in many different soil types, they can form symbiotic partnerships with soil bacteria, which we refer to as Biological Nitrogen Fixation (BNF). Magnitudes of BNF can be large in comparison to other inputs of nitrogen into ecosystems, and understanding the role that BNF plays in ecosystems is crucial to understand regional flow of nutrients [Cle+99].

There is a significant theoretical challenge in understanding how nitrogen fixation can persist. We expect that Nitrogen-fixing will be advantageous if the soil is N-limited [BM21]. However, significant BNF will increase the available nitrogen to all plants [BM21]. Nutrient transfer between fixers and non-fixers has been proposed as a mechanism which can sustain BNF despite soils being N-rich [ML17]. In this work, we develop a model based on a two-dimensional grid model in [ML17], which examined the role of root overlap and litter transfer in the soil. We extend the model to also include a dynamic soil organic matter pool, since the organic matter pool is not constant over the hundred-year simulations that I ran [Li+20]. The more realistic spatial structure allows for a greater understanding of the underlying spatial and temporal dynamics, and will serve as a foundation of future work further exploring nutrient dynamics and N fixation.

2 Model Description

2.1 Soil nutrient dynamics

We model a forest system as follows. Suppose we are in some domain $D \subset \mathbb{R}^2$. For all of our computations, we will assume that this is a square domain, $[0, L] \times [0, L] \subset \mathbb{R}^2$ folded into a torus. We keep track of two nutrients, Nitrogen (N) and Phosphorus (P). The soil contains soil-organic matter N and P (O_N, O_P), plant-available N and P (A_N, A_P), nutrient-containing leaf-litter (L_N, L_P). These (along with the plants, which we will describe later), are the state variables of our system. For each nutrient $i \in \{N, P\}$, we assume that there is an input to the available pool, I_i coming from abiotic sources. We assume that some proportion of the available nutrients, m_i, is lost from the available nutrient pool to mineralization. At any given time proportion of the litter nutrient, δ_i, decomposes, and a proportion ϵ_i of that enters the soil organic matter pool O_i. The soil organic matter pool of nutrient i loses some constant proportion k_i, of which γ_i become plant-available.

Finally, we assume that leaf litter moves according to a diffusion-advection equation with a diffusion constant D_L and advection constant $u_L = (u_L^x, u_L^y)^T$, and the distribution of available nutrients also satisfies a diffusion-advection equation with a diffusion constant D_A and advection constant $u_A = (u_A^x, u_A^y)^T$. Note that since we assume that litter moves with both nutrients together, and available nutrients move by being dissolved in groundwater, we will set the diffusion and advection constants for each nutrient type to be the same. So, without the addition of plants to the system, the leaf litter and available nutrients satisfy the following (continuous) partial differential equations:

$$\frac{\partial L_i}{\partial t} = D_L \Delta L_i - u_L \cdot \nabla L_i - \delta_i L_i \tag{1}$$

$$\frac{\partial O_i}{\partial t} = \epsilon_i \delta_i L_i - k_i O_i \tag{2}$$

$$\frac{\partial A_i}{\partial t} = D_A \Delta A_i - u_A \cdot \nabla A_i + I_i + k_i \gamma_i O_i - m_i A_i \tag{3}$$

where $\Delta = \nabla \cdot \nabla = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ is the Laplace operator and $\cdot$ is the ordinary vector dot product.

2.2 Plant growth/inputs to soil

Next, we incorporate the role of plants. Suppose there are M plants in the system. Plant j is at location (x_j, y_j). Each plant can either be a non-fixer (type 1) or a N-fixer (type 2). The only difference in what follows is that each coefficient and resulting equation may be different between type 1 and 2 (which will be indicated by a subscript depicting the type of the plant k_j).

2.2.1 Plant Growth:

Each plant j has a biomass B_j. Let the type of the plant be $k \in \{1, 2\}$ Suppose that the total amount of nitrogen and phosphorus available to the plant are N_j and P_j, respectively (these will be calculated below). We model the growth of the plant as

$$\frac{dB_j}{dt} = B_j(g_k(N_j, P_j) - \mu_k) \tag{4}$$

where g_k is the growth function of a plant of type k and μ_k is the proportion of biomass lost to turnover per unit time. Our growth function represents that each plant may be either limited by N or P:

$$g_1(N_j, P_j) = \min[\omega_{N1}\nu_{N1}N_j, \omega_{P2}\nu_{P2}P_j] \tag{5}$$

$$g_2(N_j, P_j) = \min[\omega_{N2}(\nu_{N2}N_j + F), \omega_{P2}\nu_{P2}P_j] \tag{6}$$

Here, ω_{ik} is the efficiency of the use of nutrient i by a plant of type k; ν_{ik} is the proportion of uptake of nutrient i by a plant of type k and F is the amount of nitrogen being fixed by an N-fixer type plant.

2.2.2 N Fixation:

For the amount of nitrogen being fixed, we can assume that the fixer is either obligate, meaning it fixes a constant amount of N per biomass, or facultative, meaning it fixes exactly how much is required so that it is not N-limited. Following [ML17], if fixation is perfectly facultative with a maximum rate given by $F_{\max}$, we can write

$$F = \max\left[0, \min\left[F_{\max}, \frac{\omega_{Pk}\nu_{Pk}P_j}{\omega_{Nk}} - \nu_{Nk}N_j\right]\right] \tag{7}$$

If we suppose that the fixer is obligate, we can write our growth equation for type 2 as

$$g_2(N_j, P_j) = \min[\omega_{N2}(\nu_{N2}N_j + F_O B_j), \omega_{P2}\nu_{P2}P_j] \tag{8}$$

where F_O is the rate of obligate fixing per unit biomass of the plant.

2.2.3 Available Nutrients and Rooting distribution:

Each plant takes in available nutrients of the soil through its roots. To represent this, we let $K_j = K_j(x, y)$ be a function representing the proportion of the soil accessible to the roots at a point (x, y), assuming that the tree is centered at $(0, 0)$. The function K_j should be thought of as a mathematical kernel; i.e. a nonnegative function of compact support, and it should take values in $[0, 1]$. Given that it represents the roots of a plant, it is reasonable to assume that it is radially symmetric, i.e. $K_j(x, y) = K_j(r)$ where $r = \sqrt{x^2 + y^2}$. Furthermore, it should decrease with r up to some maximum rooting radius, $R_{\max}$.

Suppose we know the rooting kernel K_j for a plant j; then we can compute the total available nitrogen to that plant as

$$N_j = \iint A_N(x, y)K_j(x - x_j, y - y_j)dxdy = \iint A_N(x, y)K_j(x_j - x, y_j - y)dxdy = (A_N * K_j)(x_j, y_j) \tag{9}$$

by the symmetry of K_j, where $(A_N * K_j)$ is a convolution. Similarly, we have that the total available phosphorus to plant j is

$$P_j = (A_P * K_j)(x_j, y_j) \tag{10}$$

It is unclear what exactly makes a reasonable rooting kernel; as a first approximation, we use the following quadratic kernel.

$$K(x, y) = \begin{cases} \frac{1}{c}(R_{\max}^2 - x^2 - y^2) & \text{if } x^2 + y^2 \le R_{\max}^2 \\ 0 & \text{if } x^2 + y^2 > R_{\max}^2 \end{cases}$$

where for an appropriate constant c which normalizes the kernel, we take

$$c = \iint_D K_j(x,y)dxdy = \int_0^{R_{\max}^2} \pi(\sqrt{R_{\max}^2 - z})^2 dz = \pi R_{\max}^4/2$$

noting that the integral of $K(x,y)$ is the solid found by rotating $z = R_{\max}^2 - x^2$ around the $z-$axis.

2.2.4 Uptake from soil

We know from equations (9, 10), how much nutrient is available to each plant; we assume that they have the ability to uptake this amount at a constant rate ν_{Nk} and ν_{Pk} (where k is the plant type). If plant j is a nonfixer and grows at a rate $\frac{dB_j}{dt} = B_j g(N_j, P_j)$, then the total amount of N actually being uptaken is equal to $\frac{B_j(g(N_j,P_j))}{\omega_{N1}}$. For a fixer, meanwhile, the amount of N uptaken from the soil is equal to $\frac{B_j(g(N_j,P_j)-\omega_{N2}F)}{\omega_{N2}}$ where F is the amount of nitrogen fixed. The amount of P uptaken for both types is is $\frac{B_j g(N_j,P_j)}{\omega_P}$. So, at any point (x,y) of the soil, the reduction in available nitrogen due to the plants is equal to

$$\frac{\partial A_N}{\partial t}(x,y) = -\sum_{j=1}^{m} K_j(x_j - x, y_j - y)\frac{B_j(g_{k_j}(N_j,P_j) - \omega_{NK_j}F_{k_j})}{\omega_{Nk_j}} \tag{11}$$

where $F_{k_j} = F$ for a fixer and 0 otherwise, and similarly for phosphorus.

2.2.5 Litterfall

The amount of turnover by each plant, as in equation (3), is just a constant proportion of the biomass, or $\mu_k B_j$. So the amount of litter N and litter P being added to the L_N from plant j of type k is $\frac{\mu_k B_j}{\omega_{Nk}}$ (and similarly for P). Turnover becomes litter according to the distribution the litter falls. Let this distribution be $f(x,y)$ (i.e., it is a probability distribution since $f(x,y) \geq 0$ and $\iint f(x,y)dxdy = 1$); then the change in leaf litter at a point (x,y) due to turnover is

$$\frac{\partial L_N}{\partial t}(x,y) = \sum_{j=1}^{M} \frac{\mu_{k_j} B_j}{\omega_{Nk_j}} f(x_j - x, y_j - y) \tag{12}$$

For our litterfall kernel, we choose an exponential distribution given by

$$f(x,y) = \frac{\lambda^2}{2\pi} e^{-\lambda\sqrt{x^2+y^2}} \tag{13}$$

for some $\lambda \in (0,\infty)$. The parameter λ determines how far away on average the leaves fall from the tree. If λ is small, they will disperse far way from the tree, while a large λ means that most of the litter falls right where the tree is.

2.3 Final System of Equations

Incorporating all of the equations thus far, we get that a continuous system which models nutrient transfer in a system with M plants at locations (x_j, y_j) is given by the following set of equations:

$$\frac{dB_j}{dt} = B_j(g_{k_j}(N_j, P_j) - \mu_{k_j}) \text{ for tree } j \text{ of type } k_j,\ j = 1, ..., M,\ k_j \in \{1, 2\} \tag{14}$$

$$\frac{\partial L_N}{\partial t} = D_L \Delta L_N - u_L \cdot \nabla L_N - \delta_N L_N + \sum_{j=1}^{M} \frac{\mu_{k_j} B_j}{\omega_{Nk_j}} f(x_j - x, y_j - y) \tag{15}$$

$$\frac{\partial O_N}{\partial t} = \epsilon_N \delta_N L_N - k_N O_N \tag{16}$$

$$\frac{\partial A_N}{\partial t} = D_A \Delta A_N - u_A \cdot \nabla A_N + I_N + k_N \gamma_N O_N - m_N A_N - \sum_{j=1}^{m} K_j(x_j - x, y_j - y) \frac{B_j(g_{k_j}(N_j, P_j) - \omega_{NK_j} F_{k_j})}{\omega_{Nk_j}} \tag{17}$$

$$\frac{\partial L_P}{\partial t} = D_L \Delta L_P - u_L \cdot \nabla L_P - \delta_P L_P + \sum_{j=1}^{M} \frac{\mu_{k_j} B_j}{\omega_{Pk_j}} f(x_j - x, y_j - y) \tag{18}$$

$$\frac{\partial O_P}{\partial t} = \epsilon_P \delta_P L_P - k_P O_P \tag{19}$$

$$\frac{\partial A_P}{\partial t} = D_A \Delta A_P - u_A \cdot \nabla A_P + I_P + k_P \gamma_P O_P - m_P A_P - \sum_{j=1}^{m} K_j(x_j - x, y_j - y) \frac{B_j(g_{k_j}(N_j, P_j))}{\omega_{Pk_j}} \tag{20}$$

Variable	Meaning
B_j	Biomass of plant j
L_N	Litter Nitrogen
L_P	Litter Phosphorus
O_N	Organic Nitrogen
O_P	Organic Phosphorus
A_N	Available Nitrogen
A_P	Available Phosphorus

Parameter	Meaning
μ_k	Rate of biomass lost by plants of type k through turnover
D_L	Diffusion coefficient of litter
D_A	Diffusion coefficient of available
u_L	Advection coefficient of litter
u_A	Advection coefficient of available
δ_i	Rate of litter decomposition of nutrient i
ω_{Nk}	Conversion of plant of type k biomass into N
ω_{Pk}	Conversion of plant of type k biomass into P
ϵ_i	Fraction of decomposed litter nutrient i becoming SOM
k_i	Rate at which SOM gets broken down
γ_i	Proportion of broken down SOM which becomes available
I_i	Rate of abiotic input of nutrient i
m_i	Rate which available nutrients are lost from the system

3 Computing the system of PD-Integral Equations in (14-20)

The systems of equations in (14-20) are far too complicated to be understood analytically, and numerical solutions are required. We used the R package ReacTran [SM12] and its tran.2D function to create a discretized finite-difference grid and compute the transport terms in the equations (the advection and diffusion). We used the R package deSolve [KTR10] and its function lsodes to compute solutions of the resulting large system of ODEs. With our code and run on a laptop with an Intel i7 core, it takes about 1 minute for a 100-year simulation of a 40 m × 40 m plot, with a 30 × 30 discretized grid. The base set of parameters was taken from two sources, namely the parameters used in [ML17] along with initial conditions derived from estimates in tropical forests in the supplemental information to [Hou+08]. We used the same distribution of plants, consisting of 16 fixers and 16 non-fixers 4 distributed on the grid evenly. The domain was folded into a torus to approximate an infinite spatial grid. We observed no issues with the numerical computation failing to converge.

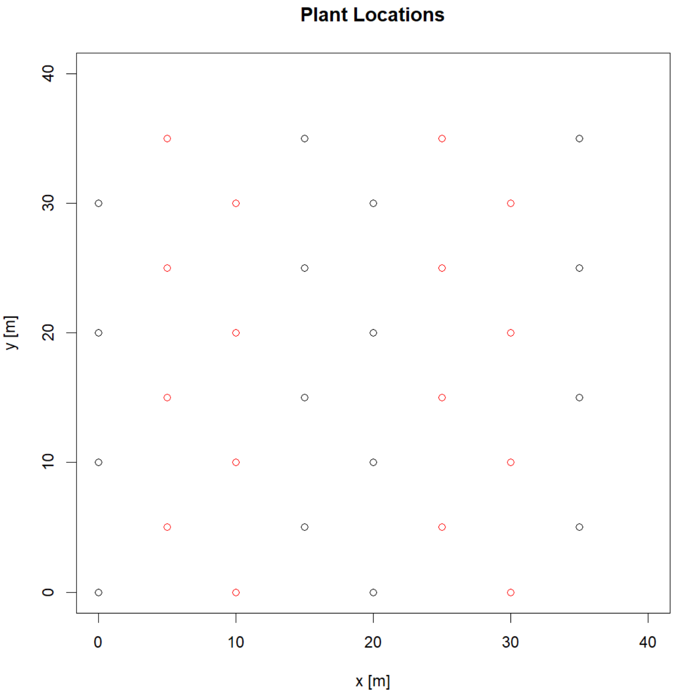
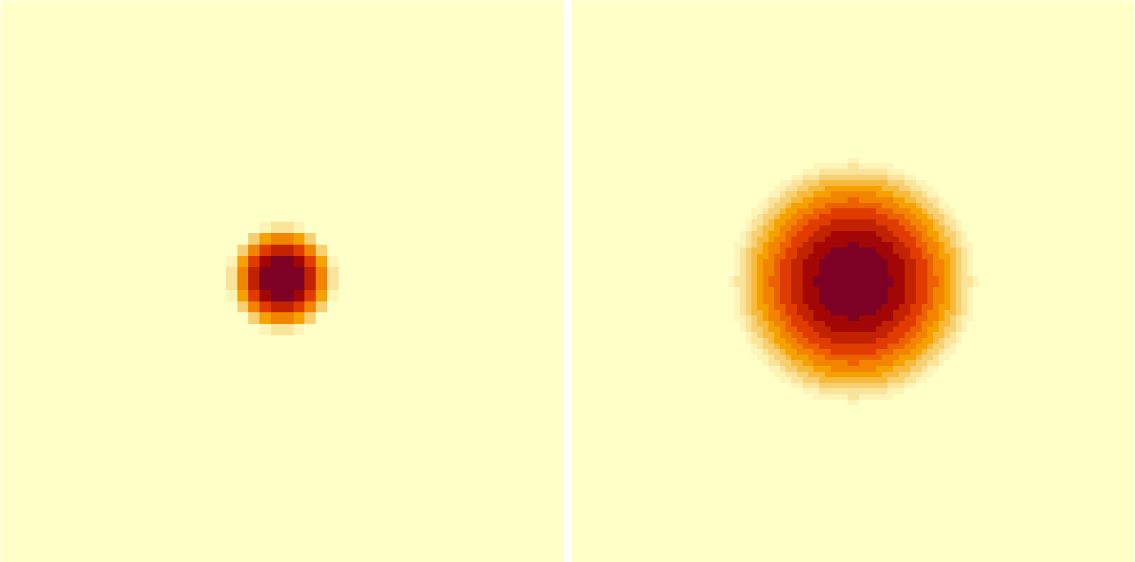


Figure 1: Red = fixer, Black = non-fixer

4 Results

Although the bulk of the project thus far has been to simply build the model itself, I started to test it by running the model for the following combinations of parameters. This allows one to evaluate the relative importance of spatial movement and root overlap in determining when N fixation with be sustained and favored over non-fixing plants. We varied the max rooting radius between a low state, set to $R_{\max} = 4$ m, and a high state, with $R_{\max} = 8$ m. There is no rooting overlap when $R_{\max} = 4$ m, while all neighbors have some overlap with $R_{\max} = 8$ m. Next, we varied the litterfall distribution. On one end, setting $\lambda = 1$ means that the litter falls far away from the tree, while setting $\lambda = 5$ means that almost all the litter falls right next to the tree, in the rooting radius. We varied turnover rates from a low rate of $\mu_1 = \mu_2 = 0.05$ yr^{-1} to a high rate of $\mu_1 = \mu_2 = 0.35$ yr^{-1}. We had a no-diffusion setting and a diffusion coefficient of $D_A = D_L = 5$ m^2/yr. We varied advection between no advection occuring and an advection vector rate of $u_L = (10 \text{ m/yr}, 0 \text{ m/yr})$.

To understand when fixing nitrogen is advantageous versus disadvantageous, we tracked the ratio of fixer biomass to non-fixer biomass over time. When this ratio is increasing, that means that fixers are doing relatively better than nonfixers, while the opposite is true when the ratio is decreasing6. For ease, we will refer to this value by $C = \frac{\text{Fixer Biomass}}{\text{Nonfixer Biomass}}$.



(a) Rooting Kernel, $R_{\max} = 4$

(b) Rooting Kernel, $R_{\max} = 8$

Figure 2: Rooting kernels for the two scenarios

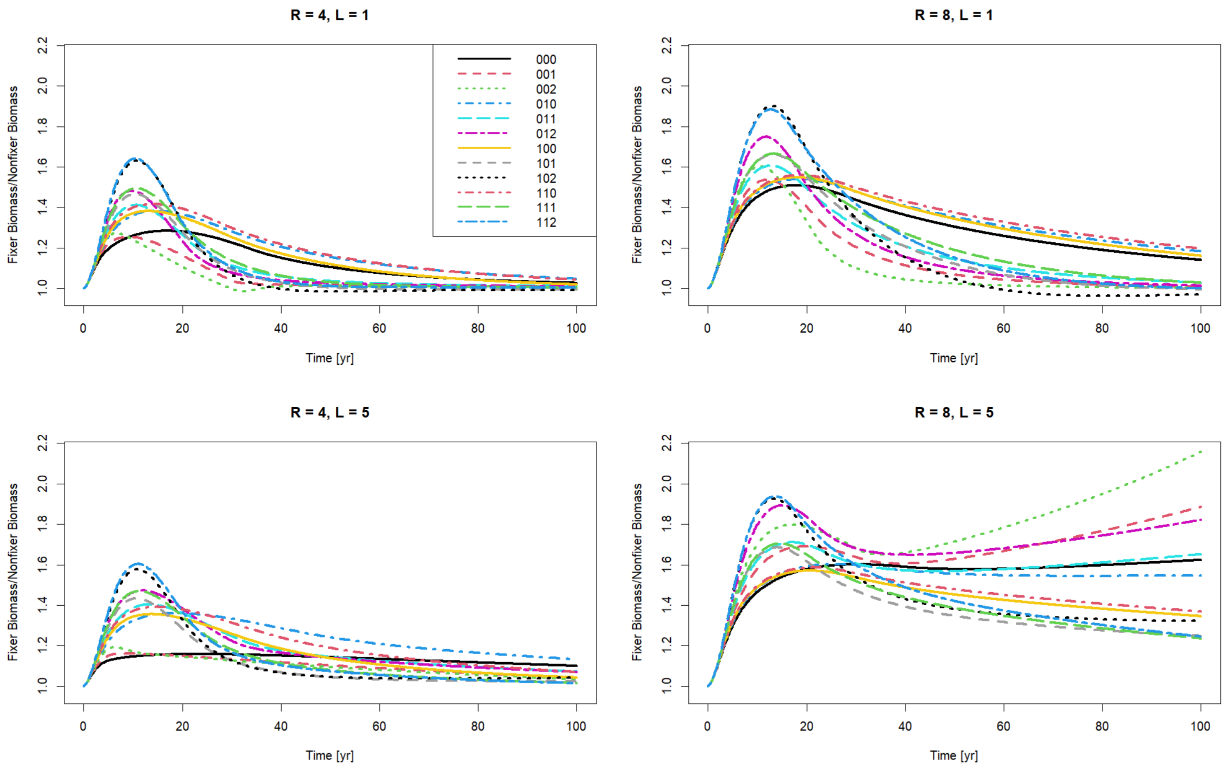


Figure 3: Comparing different rooting radius and litterfall parameters

4.1 Rooting radius and litterfall distribution

We compared the dynamics if the maximum rooting radius was large, meaning that root overlap occured, or small, meaning every plant had its own rooting zone. As we can observe in figure 3, the graphs on the left feature lower values of C than the graphs on the right, implying that fixers do better in general relative to nonfixers when the rooting radius is large rather than small. Changing the litterfall distribution had little effect on C when the rooting radius was small, but when it was larger, a higher value of $L = \lambda$ corresponded to a much higher advantage for fixers. In the scenarios with highest value of C, such as 001 (corresponding to $R = 8$, $\lambda = 5$, no advection/diffusion and $\mu_1 = \mu_2 = 0.2$, see figure 7) and 002 (corresponding to $R = 8$, $\lambda = 5$, no advection/diffusion and $\mu_1 = \mu_2 = 0.35$), the nonfixers were briefly growing quicker over years 20-40, while before and after that it is more advantageous to be a fixer. This suggests that when there is no spatial transfer of litter and a lot of litter falls right next to the tree, the relative benefits of being a Nitrogen fixer are highest.

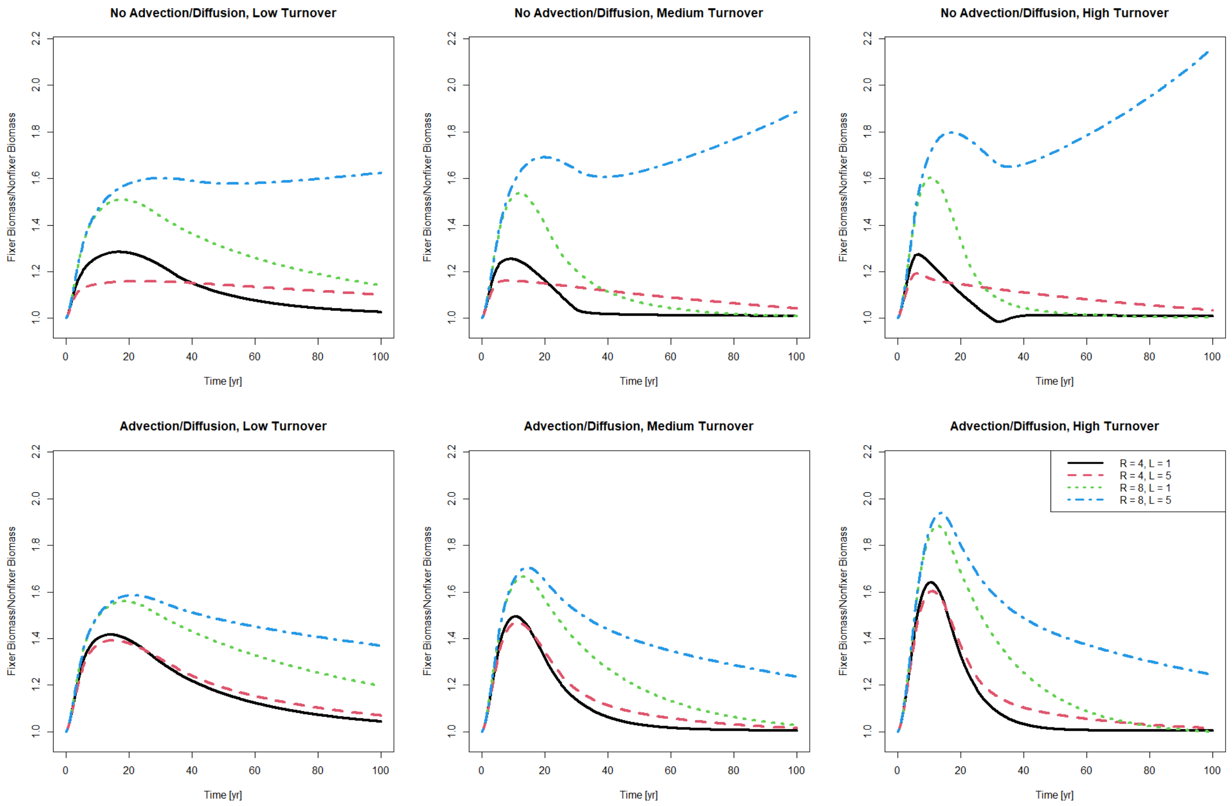


Figure 4: Comparing different litterfall rates and litter movement parameters

4.2 Turnover Rates and Litter Movement

Next, we did a similar analysis comparing no movement of litter (no advection/diffusion) versus positive advection and diffusion, at a low, medium, and high turnover rate.

We can observe a few trends. First, when the spatial transfer of litter is turned on, the fixers grow more relative to the nonfixers in the first 15-20 years. However, they also grow far less than nonfixers in the last 80 years. This suggests that litter transfer spatially through diffusion and advection is much more likely to benefit the type of plant which is already growing quicker–the competitive winners. It does not allow for the fixers to maintain their competitive advantage for any longer duration of time.

These effects are more pronounced as we increase the rate of turnover. Indeed, at the highest turnover rate, the spatial transfer of nutrients through leaf litter causes the $R = 8$, $L = 5$ to go from being better growth conditions for fixers, to entirely flipping the direction of the curve. So, the scenario which was optimal for fixers becomes far better for nonfixers in the presence of advection and diffusion. This suggests that advection and diffusion can significantly help nonfixers when the fixers have a rooting and litterfall strategy which captures the almost all nutrients in their leaf litter.

5 Further Work

The bulk of our work thus far has been on designing the system of equations themselves and numerically computing some initial solutions; there is much that we can use this model for to explore. Some general trends of parameter dependence were observed, but there is far more to analyze to understand parameter dependence. Furthermore, the initial conditions were derived from estimates of a tropical forest, while it would be quite useful and interesting to examine the role that other initial conditions would play in the dynamics, particularly given that the initial levels of soil N are known to be essential for the competitive dynamics between fixers and nonfixers [BM21]. Beyond extensions of the same work with a greater resolution of the model and its parameters, I highlight three possible future research directions.

5.1 Succession model

First, the current model does not consider any reproduction or succession in plants. The fact that plants are changing the nutrients in the soil, particularly by nitrogen fixation creating an influx of more nitrogen to the system, means that the competitive dynamics between different types of plants changes over time. We could create an ecological succession model as follows.

- Begin with a set of initial conditions and n plants which are either fixers or non-fixers
- Solve the set of equations (14-20) for one year
- Reproduce proportionally to the biomass of each type
- Reseed the grid with the new plants and initial conditions which are the current state of the soil
- Repeat and observe the frequencies of plants over time

Based on our results, which showed Nitrogen fixers having the advantage over non-fixers over the first 10-20 years while that switched afterwards, we would expect the fixers to initially be dominant. However, it is unclear at what point, if any, the non-fixers would be able to invade. This type of model would observe succession in action, and in particular could see what happens after a disturbance such as a forest fire. There are numerous models which examine the succession of N fixing plants after a disturbance, and find that the starting N supply is crucial to the dynamics which occur [BM21]. We could gain a greater understanding of ecological succession using this continuous spatial model.

5.2 Varied Litterfall

Plants have significant variation in leaf morphologies and litterfall patterns; for instance, pine trees have long needles which fall continously,, while deciduous leaves are much broader and fall seasonally. The leaf morphology and resulting litterfall pattern could be considered to be a strategy pursued by each of the plants, and we could use this model to better understand how leaf morphology can influence litter transfer, and whether Nitrogen fixation would be most advantageous under a certain leaf and litterfall type.

5.3 Different strategies of Fixation

In our model, we assumed that plants are perfectly facultative Nitrogen fixers, meaning that they fix just enough to not be limited by nitrogen, up to some maximum value. In principle, this would be the optimal way to fix Nitrogen [Men+09], but there are other possible strategies to consider. One such strategy is an obligate N fixer: one which always produces the same, constant amount of N per biomass [Men+09]. In [Men+09; MBW11], the authors examined conditions under which obligate or facultative N fixation would be favored. In particular, if there is a cost or time lag to switching fixation on or down-regulating fixation rates, it might be more advantageous to be an obligate fixer [Men+09]. We could use our continuous model to study this question and incorporate this additional set of strategies.

6 Acknowledgements

I would like to sincerely thank Professor Simon Levin for introducing me to the problem and supervising this independent work. Furthermore, I really appreciate Ari Freedman's help and collaboration, especially his skills in making figures and gifs in R. I would also like to thank Benjamin Houlton and Duncan Menge for offering very useful information on modeling these ecosystem processes, and guidance on questions to consider about the system. Finally, I would like to thank the Princeton Program in Applied and Computational Mathematics for providing the certificate program with the opportunity to pursue this research project.

7 Honor Pledge

This paper represents my own work in accordance with University regulations.

§ Daniel Bauman

References

[Cle+99] C. C. Cleveland et al. "Global patterns of terrestrial biological nitrogen (N2) fixation in natural ecosystems". English. In: *Global biogeochemical cycles* 13.2 (1999), pp. 623–645.

[Hou+08] Benjamin Z. Houlton et al. "unifying framework for dinitrogen fixation in the terrestrial biosphere". English. In: *Nature* 454.7202 (2008), pp. 327–330.

[Men+09] Duncan N. L. Menge et al. "Facultative versus Obligate Nitrogen Fixation Strategies and Their Ecosystem Consequences". In: *The American Naturalist* 174.4 (2009), pp. 465–477. (Visited on 04/11/2023).

[KTR10] Karline Soetaert, Thomas Petzoldt, and R. Woodrow Setzer. "Solving Differential Equations in R: Package deSolve". In: *Journal of Statistical Software* 33.9 (2010), pp. 1–25. DOI: `10.18637/jss.v033.i09`.

[MBW11] Duncan N. L. Menge, Ford Ballantyne, and Joshua S. Weitz. "Dynamics of nutrient uptake strategies: lessons from the tortoise and the hare". English. In: *Theoretical ecology* 4.2 (2011), pp. 163–177.

[SM12] Karline Soetaert and Filip Meysman. "Reactive transport in aquatic ecosystems: Rapid model prototyping in the open source software R". In: *Environmental Modelling Software* 32 (2012), pp. 49–60.

[ML17] Duncan N. L. Menge and Simon A. Levin. "Spatial heterogeneity can resolve the nitrogen paradox of tropical forests". In: *Ecology* 98.4 (2017), pp. 1049–1061. DOI: `https://doi-org.ezproxy.princeton.edu/10.1002/ecy.1733`. eprint: `https://esajournals-onlinelibrary-wiley-com.ezproxy.princeton.edu/doi/pdf/10.1002/ecy.1733`. URL: `https://esajournals-onlinelibrary-wiley-com.ezproxy.princeton.edu/doi/abs/10.1002/ecy.1733`.

[Li+20] Zhaolei Li et al. "Global variations and controlling factors of soil nitrogen turnover rate". In: *Earth-Science Reviews* 207 (2020), p. 103250. ISSN: 0012-8252. DOI: `https://doi.org/10.1016/j.earscirev.2020.103250`. URL: `https://www.sciencedirect.com/science/article/pii/S0012825220302968`.

[BM21] Thomas A. Bytnerowicz and Duncan N. L. Menge. "Divergent Pathways of Nitrogen-Fixing Trees through Succession Depend on Starting Nitrogen Supply and Priority Effects". English. In: *The American naturalist* 198.6 (2021), E198–E214.

8 Appendix

All code is contained in a public Github repository at:

`https://github.com/dbauman18/N-Fixation-Continuous-Model`

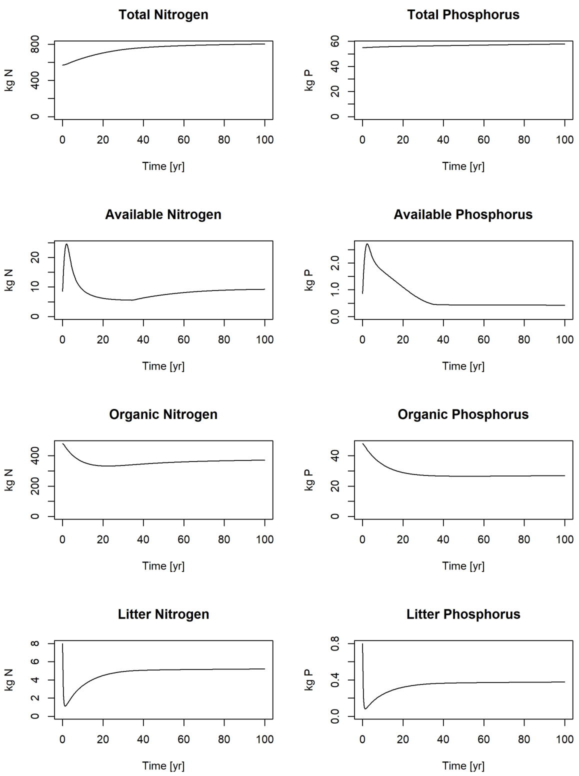
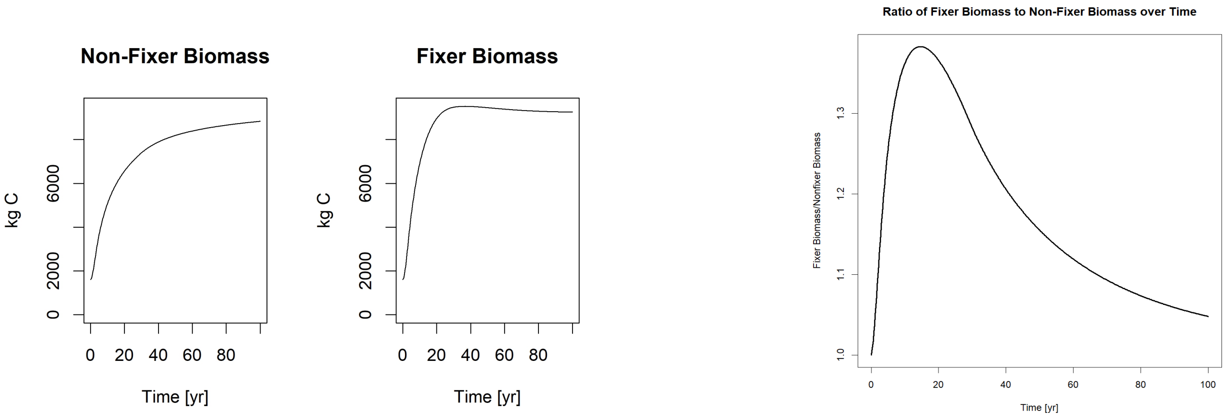


Figure 5: Nutrient pools over time with parameters given by $R_{\max} = 4$, $\lambda = 1$, $u_L = (0, 0)$, $D_L = 0$, $\mu_1 = \mu_2 = 0.05$



(a) Biomass

(b) Biomass ratio between Fixers and Nonfixers

Figure 6: The ratio of biomass captures which type does better

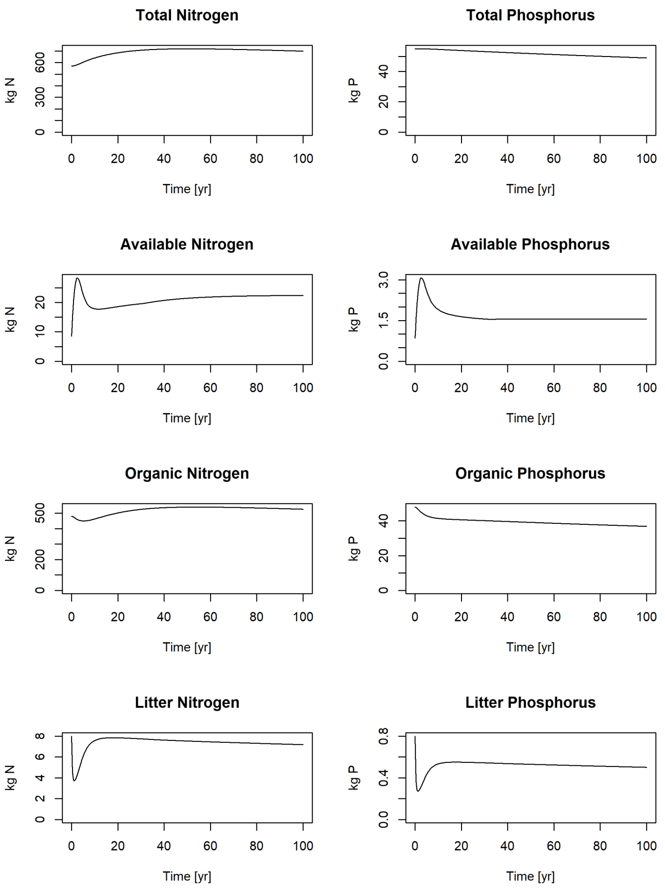


Figure 7: Nutrient pools over time with parameters given by $R_{\max} = 8$, $\lambda = 5$, $u_L = (0, 0)$, $D_L = 0$, $\mu_1 = \mu_2 = 0.2$

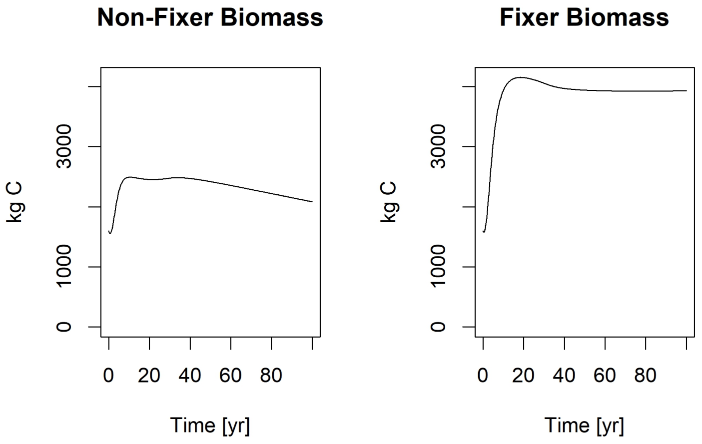


Figure 8: Biomass for the scenario in Figure 7