Ecology, 98(12), 2017, pp. 3127–3140

Why are nitrogen-fixing trees rare at higher compared to lower latitudes?

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Abstract. Symbiotic nitrogen (N) fixation provides a dominant source of new N to the terrestrial biosphere, yet in many cases the abundance of N-fixing trees appears paradoxical. N-fixing trees, which should be favored when N is limiting, are rare in higher latitude forests where N limitation is common, but are abundant in many lower latitude forests where N limitation is rare. Here, we develop a graphical and mathematical model to resolve the paradox. We use the model to demonstrate that N fixation is not necessarily cost effective under all degrees of N limitation, as intuition suggests. Rather, N fixation is only cost effective when N limitation is sufficiently severe. This general finding, specific versions of which have also emerged from other models, would explain sustained moderate N limitation because N-fixing trees would either turn N fixation off or be outcompeted under moderate N limitation. From this finding, four general hypothesis classes emerge to resolve the apparent paradox of N limitation and N-fixing tree abundance across latitude. The first hypothesis is that N limitation is less common at higher latitudes. This hypothesis contradicts prevailing evidence, so is unlikely, but the following three hypotheses all seem likely. The second hypothesis, which is new, is that even if N limitation is more common at higher latitudes, more severe N limitation might be more common at lower latitudes because of the capacity for higher N demand. Third, N fixation might be cost effective under milder N limitation at lower latitudes but only under more severe N limitation at higher latitudes. This third hypothesis class generalizes previous hypotheses and suggests new specific hypotheses. For example, greater trade-offs between N fixation and N use efficiency, soil N uptake, or plant turnover at higher compared to lower latitudes would make N fixation cost effective only under more severe N limitation at higher latitudes. Fourth, N-fixing trees might adjust N fixation more at lower than at higher latitudes. This framework provides new hypotheses to explain the latitudinal abundance distribution of N-fixing trees, and also provides a new way to visualize them. Therefore, it can help explain the seemingly paradoxical persistence of N limitation in many higher latitude forests.

Key words: ecosystem; facultative N fixers; latitude; legume; limitation; nitrogen fixation; obligate N fixers; theory; tree.

INTRODUCTION

Biological nitrogen (N) fixation is the largest natural N input to the terrestrial biosphere (Vitousek et al. 2013), and unlike other N inputs, has the capacity to respond to biotic N demand (Vitousek et al. 2002). This capacity is exceptionally high for symbioses between N-fixing bacteria and angiosperms ("rhizobial" legume species and "actinorhizal" species in other families), which can fix >100 kg N$\cdot$ha$^{-1}\cdot$yr^{-1} (Binkley et al. 1994, Ruess et al. 2009). However, at the ecosystem scale, N fixers (we call the plants "N fixers" or "N-fixing plants" regardless of whether they are actively engaged in N-fixing symbioses) can only fix N at high rates if they are relatively abundant, which they often are not.

The abundance distribution of N-fixing trees across latitude in the Americas is particularly intriguing. Forests at higher latitudes are more frequently N limited (i.e., N demand exceeds N supply) than those at lower latitudes (Vitousek and Sanford 1986, Vitousek and Howarth 1991, Hedin et al. 2009, Brookshire et al. 2012). Given that N-fixing trees can access a vast N pool that other plants cannot (atmospheric N_2), it seems reasonable that they should have a competitive advantage in N-limited habitats, and therefore be more abundant at higher latitudes. However, according to systematic government forest inventories and plot-level data from many millions of trees, N-fixing trees are 10-fold *less* abundant at higher (>35° N) than lower latitudes in the Americas (<35° N; ter Steege et al. 2006, Menge et al. 2010, 2014, 2017).

Manuscript received 20 June 2017; revised 8 September 2017; accepted 18 September 2017. Corresponding Editor: Serita D. Frey.

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High N-fixing tree abundance does not necessarily indicate high rates of symbiotic N fixation (SNF), which remain poorly quantified. Global models (Houlton et al. 2008, Wieder et al. 2015, Ri and Prentice 2017) typically suggest that SNF rates are high (tens of kg $N \cdot ha^{-1} \cdot yr^{-1}$) at lower latitudes. However, these models are typically parameterized based either on an early data synthesis (Cleveland et al. 1999) or no N fixation data at all (Wieder et al. 2015). The early data synthesis (Cleveland et al. 1999) included very few measurements of SNF at lower latitudes, and more recent studies suggest that many tropical forests with abundant N-fixing trees have low to moderate rates of SNF (Barron et al. 2011, Batterman et al. 2013, Sullivan et al. 2014). Regardless of SNF rates, however, the pattern of N-fixing tree abundance in the Americas is exceptionally strong, and although abundance itself does not indicate SNF, it does control the *capacity* for SNF. The capacity for SNF, not the current rates, will help determine how forests respond to changing environmental conditions. One-quarter of anthropogenic CO_2 emissions are currently absorbed by forests (Ciais et al. 2013), but the extent to which this will continue may depend on N availability (Hungate et al. 2003, Thornton et al. 2007, Sokolov et al. 2008, Gerber et al. 2010, Wårlind et al. 2014). Therefore, vastly different capacities for SNF at higher vs. lower latitudes could help determine future carbon storage (Batterman et al. 2013).

Why are N-fixing trees rare at higher compared to lower latitudes? Hans Jenny wrote, “The question yet to be answered is whether the frequency of leguminous trees in the tropical forests studied and the related high nitrogen gains are conditioned by equatorial climate or by the history of plant evolution” (Jenny 1950). The plant evolutionary history argument was crystallized by Crews (1999). Noting that woody legumes are much more speciose in the tropics, he suggested that something unrelated to N might constrain legume trees to lower latitudes. However, trait evolution rates suggest that over 2,500 species of higher latitude woody N-fixing legumes would be extant if SNF were widely adaptive at higher latitudes (Menge and Crews 2016). Furthermore, not all N-fixing trees are legumes (rhizobial symbioses). When actinorhizal and rhizobial trees are considered together, N-fixing trees comprise only a slightly lower fraction of taxonomic diversity at higher compared to lower latitudes in the Americas (Menge et al. 2017). Overall, plant evolutionary history is likely not the explanation.

If plant evolutionary history is not the explanation, then there must be one or more ecological explanations. Even though N-fixing trees are not necessarily fixing N all the time, their capacity for SNF is their distinguishing ecological feature, so we focus on explanations that favor SNF itself. The reasoning behind our focus draws on opposing ecological forces. On one hand, SNF must be advantageous in some environments, otherwise N-fixing plants would be outcompeted. On the other hand, there must be some constraints or costs of having the capacity to fix N, otherwise perfectly “facultative” N fixers, those that adjust SNF to balance their benefits and costs exactly, would outcompete all non-fixing plants (Menge et al. 2009*a*).

Among the ecological mechanisms that could drive the latitudinal pattern of N-fixing tree abundance, climate (Jenny’s other proposed driver) has often been invoked. N-fixing trees are more abundant in hotter (Liao et al. 2017) and more arid (Pellegrini et al. 2016, Liao et al. 2017) ecosystems, but the mechanisms underlying these patterns are not well established. One previously proposed possibility is that a direct temperature constraint on the process of N fixation confines N-fixing trees to lower latitudes (Houlton et al. 2008). However, there are reasons to question a direct temperature constraint. For instance, peak growing season temperatures, unlike mean annual temperatures, are similar across a range of latitudes. Additionally, although some nitrogenase enzymes are particularly sensitive to low temperatures (Ceuterick et al. 1978), nitrogenases from bacteria adapted to higher latitudes are less so (Prévost et al. 1987). At the organismal level, bacteria and plants have adapted to Arctic conditions well enough to fix N at rates similar to their temperate counterparts (Bordeleau and Prévost 1994). We speculate that adaptation to colder temperatures, the success of herbaceous N-fixing legumes (Bordeleau and Prévost 1994, Sprent 2009) and actinorhizal N-fixing plants (Liao et al. 2017) at higher latitudes, the high SNF rates in higher latitude plants (Binkley et al. 1994, Ruess et al. 2009), and the small temperature differences across latitude during peak growing season suggest a need to look beyond a direct temperature constraint.

Temperature could also constrain SNF indirectly. According to theory, N fixers that can adjust SNF rapidly are more competitive than those with substantial time lags (Menge et al. 2009*a*). Temperature, which influences biological kinetics, likely influences how quickly N fixers can adjust SNF, so plants that live at higher latitudes could have unavoidably longer time lags, particularly at the beginning of the growing season when temperatures are still low. Significant time lags, particularly in ecosystems with short growing seasons, might select for an “obligate” SNF strategy that maintains a constant rate of SNF, rather than a facultative SNF strategy that adjusts to N limitation (Menge et al. 2009*a*). Theory suggests that obligate N fixers are rare at the landscape scale because they are only successful in early successional habitats, whereas facultative N fixers are more abundant because they persist throughout succession (Menge et al. 2009*a*, 2014). Therefore, temperature and growing season constraints on facultative SNF could explain the rarity of N-fixing trees at higher latitudes.

A second indirect climate-related mechanism also favors obligate N fixers at higher latitudes. Sheffer et al. (2015) observed that colder temperatures lead to higher soil C:N, corresponding to lower rates of decomposition and slower release of bioavailable N in soils. If colder climates cause higher latitude forests to have larger

N deficits and recover biomass more slowly, then N limitation lasts longer, favoring the evolution of an obligate SNF strategy. Tropical forests also experience N limitation, but the condition appears limited to transient periods of rapid biomass accretion that follow disturbances (Davidson et al. 2004, 2007, Barron et al. 2011, Batterman et al. 2013). The combination of transient N limitation and rapid growth favors facultative SNF at lower latitudes (Sheffer et al. 2015).

Myriad other ecological mechanisms have been proposed to limit N fixer abundance, including preferential herbivory on N fixers (Vitousek and Howarth 1991, Ritchie and Tilman 1995, Hulme 1996, Vitousek and Field 1999, Knops et al. 2000, Menge et al. 2008, Kurokawa et al. 2010), greater demand for soil nutrients that the symbionts need to fix N (e.g., phosphorus [P] or molybdenum [Mo]; Vitousek and Howarth 1991, Vitousek and Field 1999, Uliassi and Ruess 2002), greater energy demand to pay the symbionts (Vitousek and Howarth 1991, Vitousek and Field 1999, Rastetter et al. 2001), and lower N use efficiency (Menge et al. 2008). Studies addressing these mechanisms have focused on why SNF is rare in N-limited ecosystems, in an effort to understand the paradox of sustained N limitation (Vitousek and Howarth 1991), but have not addressed how these mechanisms influence the latitudinal abundance distribution of N-fixing trees. Understanding the rarity of SNF in N-limited ecosystems is integral to the latitudinal issue, but only addresses the higher latitude end of the spectrum. Moreover, these studies focus on the process of SNF, rather than the abundance of trees capable of SNF. A full explanation for the latitudinal abundance pattern needs to address N-fixing tree abundance, and why N-fixing trees are abundant at lower latitudes as well as rare at higher latitudes.

Here, we introduce a graphical framework to understand the abundance of N-fixing trees across latitude. This framework starts by providing a general explanation for sustained N limitation to net primary productivity (synonymous with plant N demand exceeding soil N supply). Our framework then reveals four classes of hypotheses to explain the latitudinal abundance pattern of N-fixing trees. Two of these hypotheses are new, one generalizes a previously proposed mechanism and extends other previously proposed mechanisms to a latitudinal context, and the fourth is one we have previously developed and include here for completeness. The first hypothesis proposes that, contrary to current understanding, N limitation is more common at lower latitudes (*N limitation frequency hypothesis*). The second new hypothesis proposes that *more severe* N limitation is more common at lower latitudes, even if some degree of N limitation is more common at higher latitudes (*N limitation severity hypothesis*). We define N limitation severity as the degree of imbalance between plant N demand and soil N supply, so "more severe" and "more moderate" indicate directions along an N limitation axis. A third possibility is that SNF is cost effective under more moderate N limitation at lower latitudes, whereas it is only cost effective under more severe N limitation at higher latitudes (*N fixation benefit–cost hypothesis*). The N fixation benefit–cost hypothesis generalizes specific mechanisms (e.g., Houlton et al. 2008) and extends previously proposed mechanisms (e.g., preferential herbivory might limit N fixers; Vitousek and Field 1999, Menge et al. 2008) to a latitudinal context (e.g., preferential herbivory might change across latitude). A fourth possibility, which we developed previously (Menge et al. 2009*a*, 2014, Sheffer et al. 2015), is that the regulation of SNF changes with latitude (*Differential regulation hypothesis*). These hypotheses are not mutually exclusive, and each could be driven by multiple specific mechanisms.

Methods

Theoretical model

Our graphical theory is more general than one specific model, but we use a mathematical model to show how specific plant traits (in the mathematical model) determine the values of the graphical components. The mathematical model we use is simple by design, following a long tradition in theoretical ecology, not because we eschew the importance of other factors, but because including other factors would obfuscate our understanding. Because of its simplicity, our model might miss some of the specific details that more complex models would capture, but it can also give more general insights. Our results emerge from the model shown here, but they could also emerge from other models that include more realistic features. The theory we use builds on Menge et al. (2008, 2009*a*, *b*), and tracks how plant populations, B_i (kg C·ha^{-1}), a soil pool of plant-unavailable N, D (kg N·ha^{-1}), and a soil pool of plant-available N, A (kg N·ha^{-1}), change over time

$$\frac{dB_i}{dt} = B_i\left(\min\left[\omega(F_i)(\nu(F_i)A + F_i),\ \frac{g(F_i)}{1 + \gamma(F_i)\Sigma_j B_j}\right] - \mu(F_i)\right) \tag{1}$$

$$\frac{dD}{dt} = \sum\nolimits_j \frac{\mu(F_j)B_j}{\omega(F_j)} - mD - \varphi D \tag{2}$$

$$\frac{dA}{dt} = I + mD - kA - \sum\nolimits_j \frac{B_j}{\omega(F_j)}\left(\min\left[\omega(F_j)(\nu(F_j)A + F_j),\ \frac{g(F_j)}{1 + \gamma(F_j)\sum_k B_k}\right] - \omega(F_j)F_j\right). \tag{3}$$

The subscripts i, j, and k refer to different plant types. In this model (Fig. 1a), plant growth can be limited by

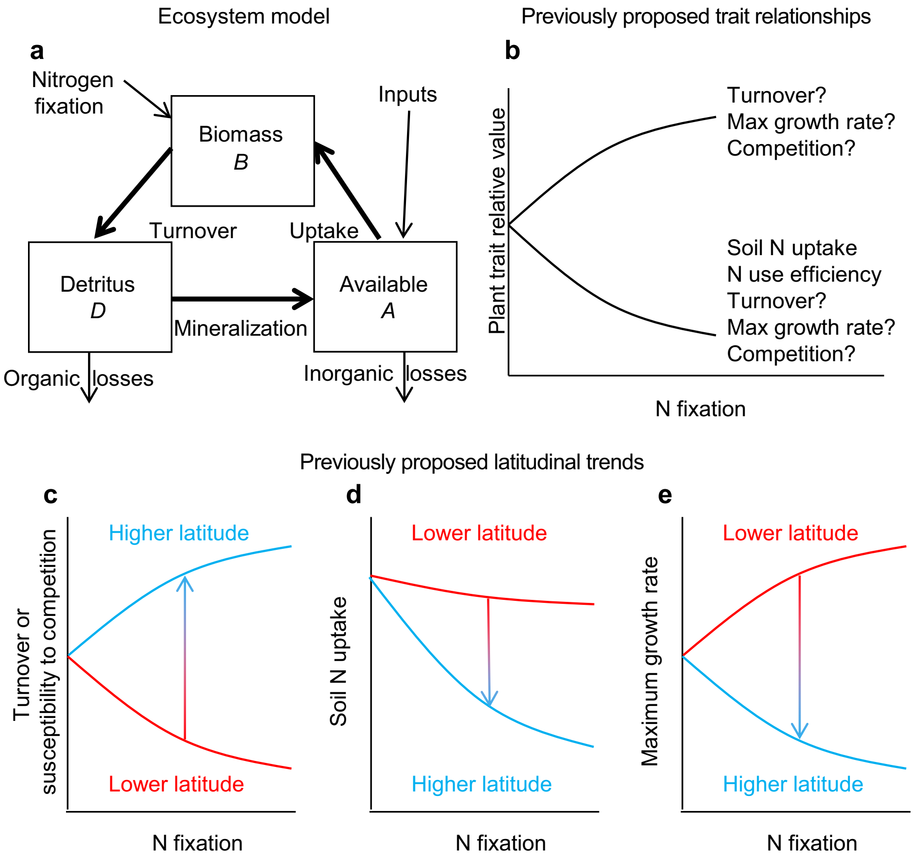


FIG. 1. Structure of the theoretical model and previously proposed trends. Red and blue curves indicate lower and higher latitudes, respectively. (a) The model is an ecosystem model that tracks nitrogen (N) in plants and soils, and carbon in plants. Plant growth can be limited by N, by another implicit resource such as light or phosphorus, or co-limited by N and the other resource. (b) Previously proposed relationships between N fixation and other plant traits. The vertical axis is a relative trait value axis for each trait, so the absolute value has no meaning. Question marks by traits indicate that there are mechanisms suggesting both directions (the trait value might increase or decrease with N fixation). (c–e) Previously proposed changes in the relationship between N fixation and plant traits across latitude. The changes indicated are changes in slope. Although some are shown as switches in the sign of the slope (e.g., up vs. down), they could also be changes in slope without a change in sign (e.g., less down vs. more down). See the "Previously proposed trade-offs between SNF and plant traits" subsection of the *Methods* for specific mechanisms underlying these trends. [Color figure can be viewed at wileyonlinelibrary.com]

N or another density-dependent factor such as light, P, or another resource.

Plant traits can vary with SNF, between non-fixing and N-fixing species regardless of fixation rate, or both. For simplicity, we only consider trait variation with SNF in the main text, so parameter values are the same for non fixers and for N-fixing species that are not fixing N (e.g., $\omega_{\text{non}} = \omega_{\text{fix}}(0) \equiv \omega_0$). This feature makes the graphical presentation of our results simpler because both non-fixing N fixers and non fixers have the same N limitation threshold. A version of the model with species-level variation, where non-fixing and N-fixing species differ independently of SNF rates, is in Appendix S1.

All plants can take N from the plant-available soil pool via uptake, v (ha·kg $\text{C}^{-1}\cdot\text{yr}^{-1}$), and N fixers can also acquire N via fixation, F (kg N·kg $\text{C}^{-1}\cdot\text{yr}^{-1}$). Newly acquired N is converted to new biomass C via N use efficiency, ω (kg C·kg N^{-1}). When not N limited, the plant grows at a maximum per capita rate g (yr^{-1}), dampened by its susceptibility to competition, γ (ha·kg C^{-1}) and its competitors' biomass C, $\sum B$. Plant biomass turns over to the soil (μ; yr^{-1}). Plant-unavailable N is converted to plant-available N (m, yr^{-1}), and lost (φ, yr^{-1}). N comes into the plant-available soil N pool from external inputs such as N deposition (I, kg N·$\text{ha}^{-1}\cdot\text{yr}^{-1}$) and is lost (e.g., leaching or gas loss) at the rate k (yr^{-1}). All parameters are strictly positive except for fixation (F), which can be 0.

Previously proposed trade-offs between SNF and plant traits

Because a given amount of root tissue can be used for either SNF or N uptake, there is probably a trade-off between SNF and soil N uptake (Rastetter et al. 2001, Menge et al. 2008, Sheffer et al. 2015, Fig. 1b): $(dv(F))/dF \equiv v' < 0$. N-fixing plants have higher average tissue N concentrations than non-fixing plants

(Fyllas et al. 2009, Nasto et al. 2014, Adams et al. 2016), which is driven in part by symbiotic bacteria, regardless of plant N demand (Wolf et al. 2017). Therefore, we assume that nutrient use efficiency decreases with SNF: $(d\omega(F))/dF \equiv \omega' < 0$. As described in the introduction, N fixers might suffer greater rates of herbivory-driven turnover than non fixers because of their high N content $(d\mu(F))/dF \equiv \mu' > 0$. On the contrary, N-fixing trees might use extra N to increase herbivore defenses (Vitousek and Field 1999, Menge et al. 2008, Menge and Chazdon 2016), which could balance or reverse the relationship between SNF and turnover: $\mu' \leq 0$.

A number of mechanisms connect SNF to energy, P, or other non-N nutrients (Vitousek and Howarth 1991, Vitousek and Field 1999, Rastetter et al. 2001, Houlton et al. 2008). Our model specifies that some other resource limits plant growth if N does not, so competition for other resources affects the non-N-limited maximum growth rate, g, or competition, γ. Under conditions when both the non fixer and the N fixer are not N limited, greater demand for energy, P, Mo, or another resource would mean that N fixers would experience a lower maximum growth rate or greater competition than non fixers: $(dg(F))/dF \equiv g' < 0, (d\gamma(F))/dF \equiv \gamma' > 0$. On the contrary, if N fixers use their higher N content to increase photosynthetic rates (Field and Mooney 1986) or water use efficiency (Adams et al. 2016), or are better able than non fixers to access P via phosphatase enzymes (Houlton et al. 2008), they could have higher maximum growth rates or a competitive advantage when both non fixers and N fixers are not N limited: $g' > 0, \gamma' < 0$.

Previously proposed latitudinal trends in plant traits and trade-offs between SNF and plant traits

If temperature constrains SNF directly (Houlton et al. 2008), then plants at higher latitudes (L) need to spend more carbon to get the same amount of N. Our model can incorporate this in two ways. First, turnover rates of N fixers might increase more with SNF, or decrease less with SNF, at higher than at lower latitudes (Fig. 1c): $(d(d\mu(F/dF))/dL > 0$. Second, the temperature effect might require a greater investment in nodules to achieve a similar SNF rate, which would decrease the carbon available for soil N uptake via roots or mycorrhizae. In this case, the N uptake rates of N fixers decrease more with SNF at higher than at lower latitudes (Fig. 1d): $(d(d\nu(F/dF))/dL < 0$. A higher turnover cost of SNF at higher latitudes $((d(d\mu(F/dF))/dL > 0)$ could also stem from N fixers being more palatable to herbivores than non fixers at higher latitudes, but less palatable than non fixers at lower latitudes (Fig. 1c).

The idea that SNF confers a greater phosphatase advantage (Houlton et al. 2008) at lower latitudes, where P is more limiting than at higher latitudes, would mean that effects of SNF on the non-N-limited growth parameters change across latitude. If P acquisition enhances the plant's maximum growth rate more at lower latitudes (Fig. 1e), $(d(dg(F/dF))/dL < 0$, whereas if P acquisition reduces competition with neighboring plants more at lower latitudes (Fig. 1c), $(d(d\gamma(F/dF))/dL > 0$. The final previously proposed mechanism involves the degree to which N-fixing plants regulate SNF in response to soil N supply vs. N demand. In this scenario, F is constant at high latitudes but variable at low latitudes.

The trends in this section represent what has been proposed previously. However, our analytical results do not depend on these assumptions, and one could evaluate the effect of other cases using our equations in Appendix S1.

Analysis: A framework to classify mechanisms that can maintain N limitation

We show our graphical results in the main text as a function of our N limitation index, which is the difference between soil N supply flux ($S = I + mD$) and N demand at a snapshot in time (Appendix S1). Because this approach focuses on the difference between N demand and N supply, the absolute values of each do not influence the presentation. However, because it is of interest to examine changes in N demand and N supply independently, we also show our graphical results as a function of soil N supply in Appendix S2.

Our approach requires three graphical components. The first is the "co-limitation threshold," the N supply level (S_{co}) that divides N limitation from non N limitation. The co-limitation threshold is equivalent to N demand. The second component is the "N fixation benefit–cost threshold," the level of N supply (S_{crit}) at which the benefit of SNF equals the cost. The benefits vs. costs of SNF are, respectively, the new biomass gained from newly fixed N vs. the new biomass lost due to the indirect effects of SNF on the other plant parameters. The N fixation benefit–cost threshold divides the region where N fixation is cost effective from the region where it is not. In the main text we give the benefit–cost threshold results for perfectly facultative SNF. In Appendix S1, we also present results for obligate SNF and with an explicit cost of being facultative. To find the facultative SNF benefit–cost threshold, we evaluate how a small amount of fixation influences the relative plant population growth rate. A positive effect indicates a net SNF benefit, and a negative effect indicates a net SNF cost, so the threshold is where this quantity equals 0: $((\partial(dB/Bdt))/\partial F)|_{F=0} = 0$. The third and final graphical component is the distribution of habitats across a gradient of N limitation.

The pattern we want to explain concerns the relative abundance of N-fixing trees, which in our model is $(B_{\mathrm{fix}})/(\Sigma B_i)$. However, we focus our analysis on three key quantities, the co-limitation threshold, the N fixation benefit–cost threshold, and the distribution of habitats, rather than relative abundance itself, for three reasons. First, these three quantities are the key determinants of the difference in relative growth rate between N-fixing trees and non-fixing trees, so they give a clear window into relative abundance, even if there is not a one-to-one correspondence. We are interested in qualitative patterns in this work (fewer N-fixing trees, not more, in an environment that is more N limited), not specific numbers. Second, studying these three quantities requires fewer assumptions than examining relative abundance itself. Modeling relative abundance requires not only a description of how the ecosystem changes (Eqs. 1–3), but also assumptions of the starting values and amount of time since the ecosystem was at those starting values. The forest ecosystems we are modeling typically range up to a couple hundred years old (Menge et al. 2014), whereas this sort of ecosystem model takes thousands of years to approach equilibrium (Menge et al. 2009*b*). Explicitly modeling a mosaic of succession would be cumbersome and would not add qualitative understanding. Third, these three quantities facilitate the graphical framework that will clarify our hypotheses and the underlying mechanisms.

Once we have the graphical framework, we examine how the three components (the co-limitation threshold, the N fixation benefit–cost threshold, and the distribution of habitats,) might vary across latitude. Because our approach uses a simple model, and focuses on graphical and analytical (but not numerical simulation) techniques, there is no need for direct parameterization of our model or for numerical sensitivity analyses. Our model reveals hypotheses that could explain the latitudinal distribution of N-fixing trees, and how underlying plant and ecosystem traits influence these hypotheses. It does not attempt to assign quantitative probabilities to them, but in the discussion we draw on relevant literature to debate the relative likelihood of the different hypotheses.

Results

Sustained N limitation: Graphical theory

Sustained N limitation seems paradoxical because intuition says that SNF should be advantageous when N limits production, and should therefore alleviate N limitation (Vitousek and Howarth 1991). Graphically, we can show this intuitive statement as a distribution of habitats along an N limitation gradient (Fig. 2a; see Appendix S2: Fig. S1a for an N supply gradient). If SNF is cost effective whenever N limits production, then N fixers fix N in habitats to the left of the dashed line. After their newly fixed N is incorporated into the soil, N supply would increase, shifting the habitat distribution to the right. In reality, many forests are N limited, as in Fig. 2a, but have no SNF, unlike Fig. 2a, which is why sustained N limitation seems paradoxical. A key assumption underlying this seeming paradox is that SNF is cost effective whenever soil N supply alone is insufficient to meet N fixers' demand. As shown below (and elsewhere; e.g., Vitousek and Field 1999, Menge et al. 2008), this does not have to be true. Fig. 2b, Appendix S2: Fig. S1b show a scenario where most habitats are N limited but SNF is only cost effective in habitats where N limitation is sufficiently severe. Next we derive the conditions under which the scenario in Fig. 2b occurs.

Sustained N limitation: Mathematical results

The co-limitation threshold (S_{co}) is the soil N supply at which plants are co-limited

$$S_{\mathrm{co}} = \frac{\left(\frac{g(F)}{1+\gamma(F)\Sigma B} - \omega(F)F\right)(k + \Sigma B\nu(F))}{\omega(F)\nu(F)} \tag{4}$$

The N fixation benefit–cost threshold (S_{crit}) for a facultative N fixer is

$$S_{\mathrm{crit}} = \frac{(\mu_0' - \omega_0)(k + \Sigma B\nu_0)^2}{\omega_0'\nu_0(k + \Sigma B\nu_0 + B\nu_0) + \omega_0\nu_0'(k + \Sigma B\nu_0 - B\nu_0)}. \tag{5}$$

The prime indicates a derivative with respect to *F*. The 0 subscripts indicate "evaluated at $F = 0$."

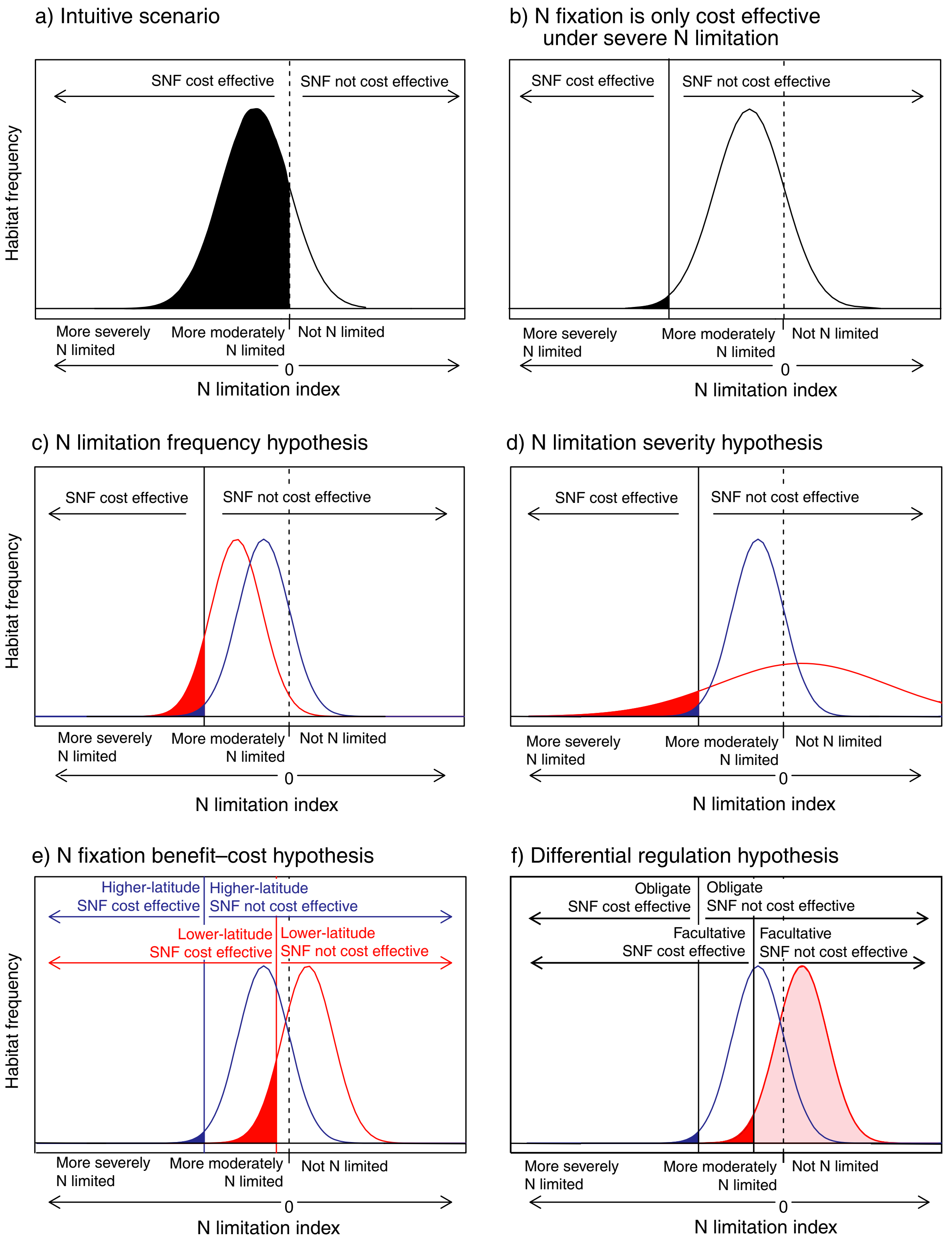
The key point of Eqs. 4–5 is that the N fixation benefit–cost threshold (S_{crit}) does not have to be the same N supply level as the co-limitation threshold (S_{co}). To see this, note that many parameters appear in only one equation. Therefore, the intuitive scenario ($S_{\mathrm{crit}} = S_{\mathrm{co}}$; Fig. 2a) is possible, but highly unlikely. By contrast, a range of N limitation where SNF is not cost effective ($S_{\mathrm{crit}} < S_{\mathrm{co}}$; Fig. 2b) is likely, depending on the values of the plant and ecosystem traits that determine the co-limitation and N fixation benefit–cost thresholds (Appendix S1: Table S1). Stronger trade-offs between SNF and N use efficiency (ω), soil N uptake (ν), or turnover (μ) lower the N fixation benefit–cost threshold, and therefore facilitate N limitation.

Comparing across latitude

We now use this graphical framework to ask: Why are N-fixing trees rare at higher compared to lower latitudes?

N limitation frequency hypothesis: N limitation is more common at lower latitudes.—The first explanation is that N limitation is more common at lower latitudes (Fig. 2c, Appendix S2: Fig. S1c), counter to our current understanding.

N limitation severity hypothesis: More severe N limitation is more common at lower latitudes.—If there is a range of N limitation over which SNF is not cost effective ($S_{\mathrm{crit}} < S_{\mathrm{co}}$, as in Fig. 2b, Appendix S2: Fig. S1b), then only the proportion of habitat where N limitation is sufficiently severe (i.e., SNF is cost effective), not the proportion that is N limited at all, predicts N-fixing tree success. The N limitation severity hypothesis states that even if N limitation is less common in lower than higher latitude forests, *more severe* N limitation is *more* common in lower than higher latitude forests (Fig. 2d, Appendix S2: Fig. S1d). Put another way, even if the mean trend is that higher latitudes are more N limited than lower latitudes, variance in the magnitude of N limitation across habitats could be greater at lower latitudes.



N fixation benefit–cost hypothesis: SNF is cost effective over a wider range of N limitation at lower latitudes

If SNF is only cost effective when N limitation is severe enough ($S_{\text{crit}} < S_{\text{co}}$; Fig. 2b), the "severe enough" threshold itself ($S_{\text{co}} - S_{\text{crit}}$) might vary across latitude. The N fixation benefit–cost hypothesis states that SNF is only cost effective under more severe N limitation at higher latitudes, whereas it is cost effective under more moderate N limitation at lower latitudes (Fig. 2e, Appendix S2: Fig. S1e). This general hypothesis class encompasses many specific mechanisms. Because plant traits modify the co-limitation threshold, the N fixation benefit–cost threshold, or both (Appendix S1: Table S1), we can determine which specific mechanisms would support the N fixation benefit–cost hypothesis (Fig. 3, Appendix S1, Appendix S2: Fig. S2). Not all of these mechanisms are likely, but we list them for completeness. First, lower N use efficiency at higher latitudes would increase the co-limitation threshold and decrease the N fixation benefit–cost threshold compared to lower latitudes. Second, stronger trade-offs between SNF and N use efficiency, soil N uptake, and turnover at higher latitudes decrease the N fixation benefit–cost threshold at higher latitudes. Third, a higher maximum growth rate, a lower susceptibility to non-N-based competition, or a lower soil N uptake rate at higher latitudes compared to lower latitudes would increase ecosystem N demand at higher latitudes.

Differential regulation hypothesis: The SNF strategy differs across latitude

The three hypotheses discussed above examine situations in which facultative N fixers are more common at lower than at higher latitudes. If higher latitude N fixers are more obligate but lower latitude N fixers are more facultative (Menge et al. 2014, Sheffer et al. 2015), then a fourth hypothesis, the differential regulation hypothesis, emerges.

Obligate N fixers are less competitive under mild N limitation than facultative N fixers, for two reasons. First, the N fixation benefit–cost threshold is closer to the co-limitation threshold for facultative (or over-regulating, under-regulating, or incompletely down-regulating; Menge et al. 2015) than for obligate N fixers (Fig. 2f, Appendix S1, Appendix S2: Fig. S1f). The second reason concerns relative growth rates when SNF is not cost effective. When SNF is not cost effective, obligate N fixers have much lower relative population growth rates than non fixers because they are wasting energy fixing N. On the contrary, facultative N fixers that are not fixing have only slightly lower relative population growth rates than do non fixers, depending on the costs of being facultative (Appendix S1).

DISCUSSION

Four general hypothesis classes emerge from our graphical framework, all of which could explain why N-fixing trees are much more abundant at lower latitudes than at higher latitudes, and all of which could act in concert. These general hypothesis classes relate to our finding that, contrary to the intuition that N fixation is cost effective under all degrees of N limitation, it is only cost effective under sufficiently severe N limitation. This finding, which has also been shown or suggested in previous studies (e.g., Vitousek and Howarth 1991, Ritchie and Tilman 1995, Vitousek and Field 1999, Rastetter et al. 2001, Menge et al. 2008), provides a graphical explanation for sustained N limitation, which has long been viewed as a

FIG. 2. Framework for visualizing the mechanisms that can explain persistent N limitation and the hypotheses that can explain the latitudinal paradox. The horizontal axis, the N limitation index, is the difference between instantaneous soil N supply and N demand (in units such as kg $\text{N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$). It represents N limitation to growth for both non fixers and N fixers that are not fixing, which in our model are equal, and therefore to net primary productivity. The vertical axis is the frequency of habitats (in proportion of area). Black, red, or blue shading indicates that the relative population growth rate of facultative N fixers exceeds that of non fixers. The dashed vertical line at 0, the co-limitation threshold, corresponds to where N supply matches N demand. Habitats to the right of the dashed line are N rich and those to the left are N limited. Habitats immediately to the left of the dashed line are only moderately N limited, whereas those further to the left are more severely N limited. SNF indicates symbiotic N fixation. (a) If N fixation is cost effective whenever N fixers are N limited, the N supply rate at which the benefits of N fixation equal the costs of N fixation is the same as the co-limitation threshold. Alternatively, (b) if N fixation is only cost effective when N limitation is sufficiently severe, there is a benefit–cost threshold to the left of the co-limitation threshold. In panel a, most of the habitat is N limited and N fixation is cost effective whenever N is limiting. Panel b shows a scenario where most habitats are N limited but N fixation is only cost effective when N limitation is sufficiently severe. This scenario can arise from a number of mechanisms (see the "Sustained N limitation: Mathematical Results" section of the *Results*). Panels represent snapshots in time. Habitats are not defined at a particular spatial scale; they could be different forests across a continent or different patches across a forest. Lower latitude distributions and benefit–cost thresholds are shown in red, higher latitude distributions and benefit–cost thresholds are shown in blue. Panels c–f show four hypotheses that can account for greater abundance of N fixers at lower latitudes. (c) N limitation frequency hypothesis: N limitation is more common at lower latitudes. (d) N limitation severity hypothesis: More severe N limitation is more common at lower latitudes, even though some degree of N limitation is more common at higher latitudes. (e) N fixation benefit–cost hypothesis: The N fixation benefit–cost threshold is at more moderate N limitation at lower latitudes, so N fixation is cost effective across a wider range of N limitation at lower latitudes. In panels c–e, the benefit–cost thresholds are shown for facultative N fixation only, whereas in panel f, different thresholds are shown for facultative and obligate N fixation. (f) Differential regulation hypothesis: Facultative N fixation is more cost effective than obligate N fixation (provided there is minimal cost to being facultative), and N fixers can be somewhat abundant even in habitats where N fixation is not cost effective because they turn fixation off (indicated by pink shading). The facultative and obligate thresholds do not need to correspond to latitude, so they are written in black. [Color figure can be viewed at wileyonlinelibrary.com]

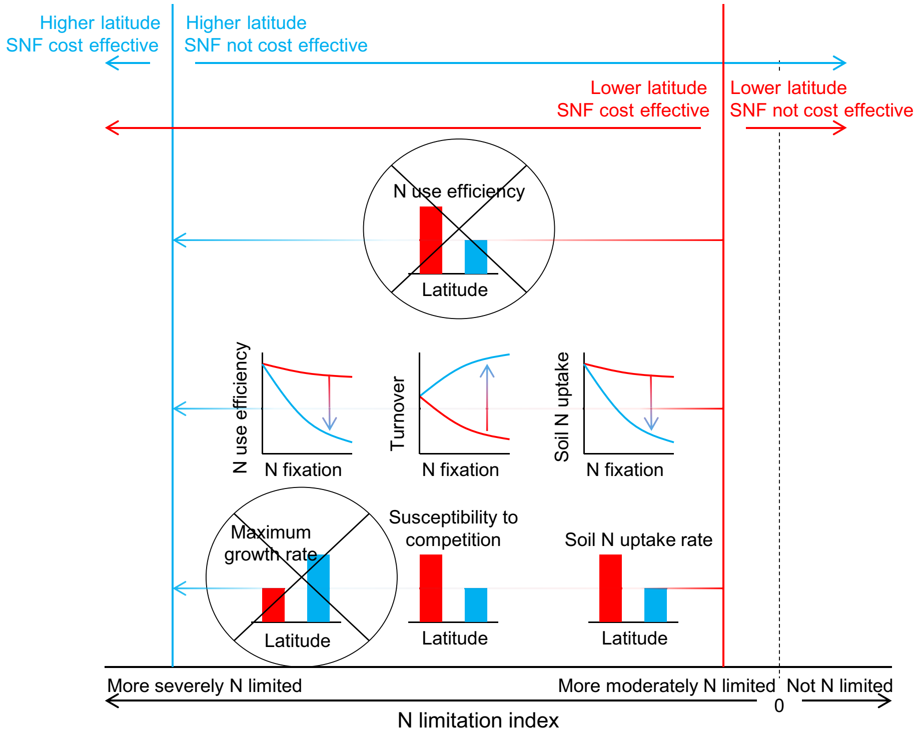


Fig. 3. Trends that would support the N fixation benefit–cost hypothesis. The horizontal axis is the same as Fig. 2. As in Fig. 2c–f, red and blue indicate lower and higher latitudes, respectively. SNF indicates symbiotic N fixation. Supporting the N fixation benefit–cost hypothesis means increasing the separation between the co-limitation threshold and the N fixation benefit–cost threshold at higher latitudes compared to lower latitudes (Fig. 2e). Arrows going from red to blue indicate this increasing separation with latitude. Either raising the co-limitation threshold (increasing N demand) or lowering the N fixation benefit–cost threshold (making N fixation less cost effective) at higher latitudes support the N fixation benefit–cost hypothesis. The top row (N use efficiency) both raises the co-limitation threshold and lowers the N fixation benefit–cost threshold. The middle row (trade-offs between N fixation and plant traits) only lowers the N fixation benefit–cost threshold. The turnover and soil N uptake trends correspond to Fig. 1c, d. The bottom row only raises the co-limitation threshold. Trends that would support the benefit–cost hypothesis but are unlikely are crossed out. [Color figure can be viewed at wileyonlinelibrary.com]

paradox in ecosystem ecology (Vitousek and Howarth 1991). Although this understanding of sustained N limitation opens doors to many questions, our focus here is on understanding the latitudinal abundance pattern of N-fixing trees in the Americas. In that vein, we now draw on the literature to evaluate how likely each general hypothesis class is and which of the specific mechanisms we have highlighted might underlie them.

N limitation is probably not more common at lower latitudes

The latitudinal abundance pattern of N-fixing trees seems paradoxical (Houlton et al. 2008, Hedin et al. 2009, Menge et al. 2014) precisely because N limitation is thought to be less common at lower latitudes, not more common (Vitousek and Sanford 1986, Hedin et al. 2009, Brookshire et al. 2012). The evidence for this, such as the 10-fold greater leaching of plant-available N in tropical compared to temperate forests (Hedin et al. 2009, Brookshire et al. 2012), suggests that our first hypothesis, the N limitation frequency hypothesis, is unlikely. Somewhat surprisingly, a meta-analysis of N fertilization studies found that N limitation was at least as strong in tropical forests as in temperate forests (LeBauer and Treseder 2008), although three factors mitigate this finding. First, few fertilization studies have been conducted in tropical forests, particularly before 2008. Second, site selection bias towards young and successional tropical forests may have amplified the N limitation signal compared to the true distribution of tropical forest types (LeBauer and Treseder 2008). In particular, only one mature tropical forest was included in that meta-analysis, and it did not show an NPP response to N fertilization. Mature tropical forests, which comprise 58% of Latin American tropical forest area (Chazdon et al. 2016), are the tropical forests typically thought to be N rich (Hedin et al. 2009). Studies in mature tropical forest studies since 2008 have found no ecosystem-level response to N additions (Wright et al. 2011, Alvarez-Clare et al. 2013). Many other tropical forests, such as those growing on young substrates (Vitousek and Farrington 1997) or those in early successional stages (Davidson et al. 2004, Batterman et al. 2013), are often N limited. Third, the response metric used, the response ratio, does not distinguish between the frequency and severity of N limitation, and as we discuss below, tropical forests might be more severely but less frequently N limited.

More severe N limitation might be more common at lower latitudes

The N limitation severity hypothesis, which states that more severe N limitation is more common in lower than higher latitude forests, is new, and is an intriguing possibility. It could explain why tropical forests appeared at least as N limited as temperate forests in a meta-analysis (LeBauer and Treseder 2008). Even if most tropical forests are not N limited, a few severely N-limited forests would inflate the average response to fertilization. On a mechanistic level, lower latitude forests likely have a greater capacity for more severe N limitation than higher latitude forests. Longer growing seasons, warmer temperatures, and ample rainfall stimulate N demand, so if N supply is greatly diminished, for example, due to large disturbance-mediated N losses, then lower latitude forests can be more severely N limited than higher latitude forests (Fig. 2d). For example, a recent modeling study (Ri and Prentice 2017) suggests that N demand that is unmet by recycling is much higher at lower than higher latitudes.

Variation in N limitation could occur at a variety of scales. On the successional timescale and the landscape spatial scale, a variety of studies suggest that N limitation, possibly severe N limitation, is common in young regenerating tropical forests (Davidson et al. 2004, 2007, Batterman et al. 2013), which comprise 22% of Neotropical forests (where "young" is <20 yr old; Chazdon et al. 2016). However, N-fixing trees are also common in mature tropical forests (ter Steege et al. 2006, Batterman et al. 2013, Menge and Chazdon 2016). On smaller spatial scales, tree-fall gaps lead to greater understory light penetration at lower latitudes because of the sun angle (Canham et al. 1990). Greater light penetration, which increases N demand for the remaining trees, combined with reduced N supply in gaps (Vitousek and Denslow 1986) could drive a severe N demand-supply imbalance in gaps, even in mature forests. A study in Panama documented much higher nodulation rates in mature forest gaps than in the surrounding matrix (Barron et al. 2011), which could explain the continued success of N-fixing trees in mature tropical forests (Batterman et al. 2013).

SNF might be cost effective under a wider range of N limitation at lower latitudes

Most of the previously proposed mechanisms that could constrain N fixers in N-limited environments are, in essence, explanations for why SNF is only cost effective when N limitation is sufficiently severe. An allocation trade-off between soil N uptake and SNF (Rastetter et al. 2001, Menge et al. 2008), lower N use efficiency or higher turnover as a consequence of SNF (Menge et al. 2008), and energetic or other resource (e.g., P or Mo) costs of SNF (Vitousek and Howarth 1991, Vitousek and Field 1999, Rastetter et al. 2001, Uliassi and Ruess 2002) all make SNF cost effective under more severe but not more moderate N limitation (Fig. 2b).

If any of these specific mechanisms change across latitude, and the change is in the right direction, they could support the N fixation benefit–cost hypothesis, and help explain why N fixers are rare at higher latitudes. Two of these latitudinal changes relate to previously proposed mechanisms (Fig. 3). If temperature constrains the process of SNF (Houlton et al. 2008), then higher latitude N fixers would need to invest more carbon per unit N fixed than lower latitude N fixers. Such a carbon investment could strengthen the trade-off between SNF and N uptake at higher latitudes because carbon used for SNF cannot be used for soil N uptake. Alternatively, such a carbon investment could make SNF more costly via an increased turnover rate.

The second previously proposed mechanism relates to herbivory. As explained above, N fixers' higher N content could lead to higher herbivore pressure (if it is used for tasty, non-defensive compounds; Vitousek and Howarth 1991), or it could enable a greater capacity for chemical defense, by using N-based defensive compounds, by using their higher photosynthetic rates to synthesize more C-based defensive compounds, or both. If herbivory is a stronger selective force at lower latitudes (Coley and Barone 1996), then lower latitude N fixers might have been selected for greater investment in anti-herbivore defense than higher latitude N fixers (Vitousek and Field 1999, Menge et al. 2008). In this case, N fixers might have a higher turnover cost of SNF, corresponding to higher mortality rates than non fixers, at higher latitudes, but vice versa at lower latitudes (Figs. 1c, 3). In support of this prediction, N-fixing trees in the coterminous United States had higher mortality rates than non-fixing trees (Liao and Menge 2016), whereas N-fixing trees in Costa Rica had lower mortality than non-fixing trees (Menge and Chazdon 2016). This empirical mortality pattern is consistent with an herbivory mechanism, but does not pinpoint herbivory as the mechanism because herbivory was not measured.

Curiously, one previously proposed specific mechanism, that N fixers have a greater ability to produce P-liberating phosphatases (Houlton et al. 2008), cannot explain N fixer abundance in our model. The model that produced that hypothesis (Wang et al. 2007, Houlton et al. 2008) is much more complex than ours, so it is not surprising that it allows for possibilities that ours does not, but we note that many other specific mechanisms emerge from our model despite its simplicity.

In addition to the previously proposed mechanisms that could underlie the N fixation benefit–cost hypothesis, three other possibilities emerge from our model (Fig. 3). First, the stronger the trade-off between SNF and N use efficiency, the more severe N limitation must be to favor SNF (Fig. 3). Second, trees might experience weaker competition for non-N resources at higher latitudes. Third, trees might have lower soil N uptake rates at higher latitudes. However, even if these traits and trade-offs change in the right direction, they can be offset by other trends. For example, trees are more N use efficient at higher latitudes (Vitousek 1984, McGroddy et al. 2004), which lowers ecosystem-level N demand and enhances the benefit of fixed N (Fig. 3).

Although it is useful to think through these specific mechanisms, pinning down all the conditions needed to scale up to the overall balance of N fixation benefits and costs is challenging. The specific mechanisms interact, and trends for seemingly unrelated traits can cancel each other out (Appendix S1: Eq. S11). Pursuing each of these specific mechanisms is a good goal, but a complementary way to evaluate the N fixation benefit–cost hypothesis is to test the theoretical predictions rather than the parameters. For example, Menge et al. (2015) found that a number of herbaceous plant species were “over-regulators.” These plants turned SNF off at N supply levels that were lower than their N demand, as predicted by our theory (Appendix S1, Appendix S1: Fig. S1). If these plants’ SNF rates accurately assess the cost effectiveness of SNF, then “over-regulation” is evidence that the N fixation benefit–cost threshold is lower than the co-limitation threshold.

N-fixing trees might be more facultative at lower latitudes

A variety of field observations suggest that higher latitude N-fixing trees are obligate (Mead and Preston 1992, Binkley et al. 1994, Menge and Hedin 2009), whereas lower latitude N-fixing trees are facultative (Pearson and Vitousek 2001, Barron et al. 2011, Batterman et al. 2013, Sullivan et al. 2014, Bauters et al. 2016, see also Andrews et al. 2011). Modeling suggests that a strategy transition across latitude can explain the latitudinal trend (Menge et al. 2014). Underlying climate effects on soil N deficits (Sheffer et al. 2015) or on the constraints and costs of regulating SNF (Menge et al. 2009*a*) can explain a transition in strategy. Although

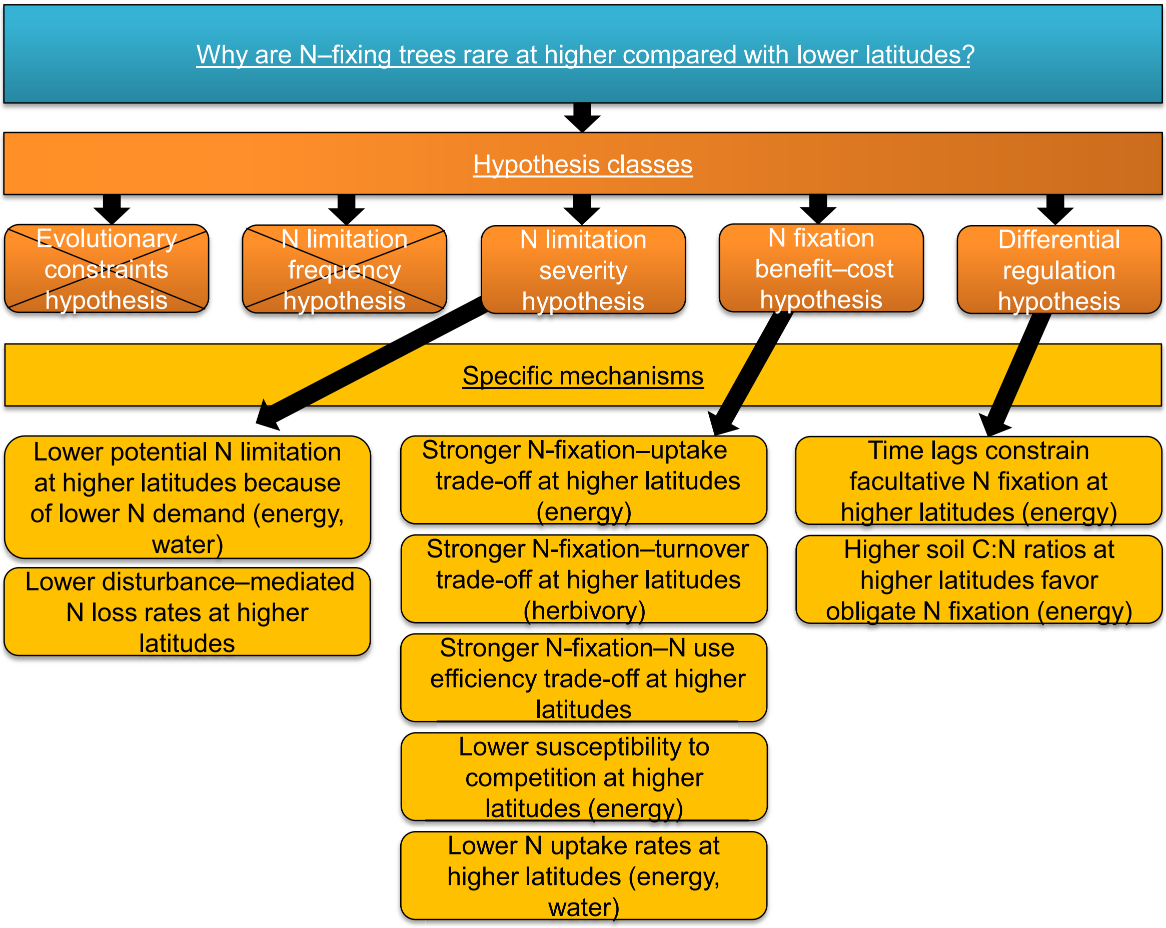


FIG. 4. Conceptual diagram of general hypothesis classes and specific mechanisms to explain the rarity of N-fixing trees at higher latitudes compared to lower latitudes. Questions are shown in blue, hypothesis classes in orange, and specific mechanisms for each hypothesis in yellow. Underlying drivers of specific mechanisms are in parentheses. Crossed out hypotheses are unlikely. Detailed explanations for each part of this figure can be found in the *Introduction, Results, and Discussion*. [Color figure can be viewed at wileyonlinelibrary.com]

experimental evidence is still scant, the differential regulation hypothesis is promising.

CONCLUSIONS

Given current evidence, the most likely reasons that N-fixing trees are more abundant at lower latitudes in the Americas are: a greater prevalence of more severe N limitation at lower latitudes (the N limitation severity hypothesis), lower costs of SNF compared with other forms of N uptake at lower latitudes (the N fixation benefit–cost hypothesis), and a transition in SNF strategy across latitude (the differential regulation hypothesis) (Fig. 4). Evolutionary constraints on the biogeography of N-fixing trees and a higher frequency of N limitation at lower latitudes are unlikely to explain the latitudinal trend of N fixer abundance in the Americas. Disentangling the relative importance of N limitation severity, N fixation benefits vs. costs, and differential regulation, and determining the specific mechanisms that underlie them, will help resolve the seemingly paradoxical latitudinal distribution of N fixers that has puzzled scientists for over 65 yr. Furthermore, given the importance of N fixation for ecosystems' responses to rising atmospheric CO_2 and temperature, testing these hypotheses will greatly improve our understanding of how the fixation and carbon sequestration responses differ across latitude, which will improve our predictions of global climate change.

ACKNOWLEDGMENTS

This material is based on work supported by the National Science Foundation under grant no. DEB-1457650. S. A. Batterman was supported by a UK Natural Environment Research Council Independent Research Fellowship (NE/M019497/1).

LITERATURE CITED

Adams, M. A., T. L. Turnbull, J. I. Sprent, and N. Buchmann. 2016. Legumes are different: leaf nitrogen, photosynthesis, and water use efficiency. Proceedings of the National Academy of Sciences USA 113:4098–4103.

Alvarez-Clare, S., M. C. Mack, and M. Brooks. 2013. A direct test of nitrogen and phosphorus limitation to net primary productivity in a lowland tropical wet forest. Ecology 94: 1540–1551.

Andrews, M., E. K. James, J. I. Sprent, R. M. Boddey, E. Gross, and F. B. dos Reis Jr. 2011. Nitrogen fixation in legumes and actinorhizal plants in natural ecosystems: values obtained using ^{15}N natural abundance. Plant Ecology & Diversity 4:131–140.

Barron, A. R., D. W. Purves, and L. O. Hedin. 2011. Facultative nitrogen fixation by canopy legumes in a lowland tropical forest. Oecologia 165:511–520.

Batterman, S. A., L. O. Hedin, M. van Breugel, J. Ransijn, D. J. Craven, and J. S. Hall. 2013. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. Nature 502: 224–227.

Bauters, M., N. Mapenzi, E. Kearsley, B. Vanlauwe, and P. Boeckx. 2016. Facultative nitrogen fixation in legumes in the central Congo basin is downregulated during late successional stages. Biotropica 48:281–284.

Binkley, D., K. Cromack Jr, and D. D. Baker. 1994. Nitrogen fixation by red alder: biology, rates and controls. Pages 57–72 *in* D. Hibbs, D. DeBell and R. Tarrant, editors. The biology and management of red alder. Oregon State University Press, Corvallis, Oregon, USA.

Bordeleau, L. M., and D. Prévost. 1994. Nodulation and nitrogen fixation in extreme environments. Plant and Soil 161:115–125.

Brookshire, E. N. J., S. Gerber, D. N. L. Menge, and L. O. Hedin. 2012. Large losses of inorganic nitrogen from tropical rainforests suggests a lack of nitrogen limitation. Ecology Letters 15:9–16.

Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20:620–631.

Ceuterick, F., J. Peeters, K. Heremans, H. de Smedt, and H. Olbrechts. 1978. Effect of high pressure, detergents and phospholipase on the break in the Arrhenius plot of *Azotobacter* nitrogenase. European Journal of Biochemistry 87:401–407.

Chazdon, R. L., et al. 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Science Advances 2:1501639.

Ciais, P., et al. 2013. Carbon and other biogeochemical cycles. Pages 465–570 *in* T. F. Stocker, et al., editors. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.

Cleveland, C. C., et al. 1999. Global patterns of terrestrial biological nitrogen (N_2) fixation in natural ecosystems. Global Biogeochemical Cycles 13:623–645.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305–335.

Crews, T. E. 1999. The presence of nitrogen fixing legumes in terrestrial communities: evolutionary vs. ecological considerations. Biogeochemistry 46:233–246.

Davidson, E. A., et al. 2004. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecological Applications 14:S150–S163.

Davidson, E. A., et al. 2007. Recuperation of nitrogen cycling in Amazonia forests following agricultural abandonment. Nature 447:995–998.

Field, C. B., and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. Pages 25–55 *in* T. J. Givnish, editor. The economy of plant form and function. Cambridge University Press, Cambridge, UK.

Fyllas, N. M., et al. 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. Biogeosciences 6:2677–2708.

Gerber, S., L. O. Hedin, M. Oppenheimer, S. W. Pacala, and E. Shevliakova. 2010. Nitrogen cycling and feedbacks in a global dynamic land model. Global Biogeochemical Cycles 24:GB1001.

Hedin, L. O., E. N. J. Brookshire, D. N. L. Menge, and A. R. Barron. 2009. The nitrogen paradox in tropical forest ecosystems. Annual Review of Ecology Evolution and Systematics 40:613–635.

Houlton, B. Z., Y. Wang, P. M. Vitousek, and C. B. Field. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. Nature 454:327–330.

Hulme, P. E. 1996. Herbivores and the performance of grassland plants: a comparison of arthropod, mollusk and rodent herbivory. Journal of Ecology 84:43–51.

Hungate, B. A., J. S. Dukes, M. R. Shaw, Y. Luo, and C. B. Field. 2003. Nitrogen and climate change. Science 302:1512–1513.

Jenny, H. 1950. Causes of the high nitrogen and organic matter content of certain tropical forest soils. Soil Science 69:63–69.

Knops, J. M. H., M. E. Ritchie, and D. Tilman. 2000. Selective herbivory on a nitrogen fixing legume (*Lathyrus venosus*) influences productivity and ecosystem nitrogen pools in an oak savanna. Écoscience 7:166–174.

Kurokawa, H., D. A. Peltzer, and D. A. Wardle. 2010. Plant traits, leaf palatability and litter decomposability for co-occurring woody species differing in invasion status and nitrogen fixation ability. Functional Ecology 24:513–523.

LeBauer, D. S., and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89:371–379.

Liao, W., and D. N. L. Menge. 2016. Demography of symbiotic nitrogen-fixing trees explains their rarity and successional decline in temperate forests. PLoS ONE 11:e0164522.

Liao, W., D. N. L. Menge, J. W. Lichstein, and G. Ángeles-Pérez. 2017. Global climate change will increase the abundance of symbiotic nitrogen-fixing trees in much of North America. Global Change Biology 23:4777–4787. https://doi.org/10.1111/gcb.13716

McGroddy, M. E., T. Daufresne, and L. O. Hedin. 2004. Scaling of C:N: P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. Ecology 85:2390–2401.

Mead, D. J., and C. M. Preston. 1992. Nitrogen fixation in Sitka alder by ^{15}N isotope dilution after eight growing seasons in a lodgepole pine site. Canadian Journal of Forest Research 22: 1192–1194.

Menge, D. N. L., and R. L. Chazdon. 2016. Higher survival drives the success of nitrogen-fixing trees through succession in Costa Rican rainforests. New Phytologist 209:965–977.

Menge, D. N. L., and T. E. Crews. 2016. Can evolutionary constraints explain the rarity of nitrogen-fixing trees in high-latitude forests? New Phytologist 211:1195–1201.

Menge, D. N. L., and L. O. Hedin. 2009. Nitrogen fixation in different biogeochemical niches along a 120,000-year chronosequence in New Zealand. Ecology 90:2190–2201.

Menge, D. N. L., S. A. Levin, and L. O. Hedin. 2008. Evolutionary trade-offs can select against nitrogen fixation and thereby maintain nitrogen limitation. Proceedings of the National Academy of Sciences USA 105:1573–1578.

Menge, D. N. L., S. A. Levin, and L. O. Hedin. 2009*a*. Facultative versus obligate nitrogen fixation strategies and their ecosystem consequences. American Naturalist 174:465–477.

Menge, D. N. L., S. W. Pacala, and L. O. Hedin. 2009*b*. Emergence and maintenance of nutrient limitation over multiple timescales in terrestrial ecosystems. American Naturalist 173:164–175.

Menge, D. N. L., J. L. DeNoyer, and J. W. Lichstein. 2010. Phylogenetic constraints do not explain the rarity of nitrogen-fixing trees in late-successional temperate forests. PLoS ONE 5:e12056.

Menge, D. N. L., J. W. Lichstein, and G. Ángeles-Pérez. 2014. Nitrogen fixation strategies can explain the latitudinal shift in nitrogen-fixing tree abundance. Ecology 95:2236–2245.

Menge, D. N. L., A. A. Wolf, and J. L. Funk. 2015. Diversity of nitrogen fixation strategies in Mediterranean legumes. Nature Plants 1:15064.

Menge, D. N. L., S. A. Batterman, W. Liao, B. N. Taylor, J. W. Lichstein, and G. Ángeles-Pérez. 2017. Nitrogen-fixing tree abundance in higher-latitude North America is not constrained by diversity. Ecology Letters 20:842–851.

Nasto, M. K., S. Alvarez-Clare, Y. Lekberg, B. W. Sullivan, A. R. Townsend, and C. C. Cleveland. 2014. Interactions among nitrogen fixation and soil phosphorus acquisition strategies in lowland tropical rain forests. Ecology Letters 17: 1282–1289.

Pearson, H. L., and P. M. Vitousek. 2001. Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. Ecological Applications 11:1381–1394.

Pellegrini, A. F. A., A. C. Staver, L. O. Hedin, T. Charles-Dominique, and A. Tourgee. 2016. Aridity, not fire, favors nitrogen-fixing plant across tropical savanna and forest biomes. Ecology 97:2177–2183.

Prévost, D., H. Antoun, and L. M. Bordeleau. 1987. Effects of low temperature on nitrogenase activity in sanfoin (*Onobrychis viciifolia*) nodulated by arctic rhizobia. FEMS Microbiology Ecology 45:205–210.

Rastetter, E. B., P. M. Vitousek, C. B. Field, G. R. Shaver, D. Herbert, and G. I. Ågren. 2001. Resource optimization and symbiotic nitrogen fixation. Ecosystems 4:369–388.

Ri, X., and I. C. Prentice. 2017. Modelling the demand for new nitrogen fixation by terrestrial ecosystems. Biogeosciences 14:2003–2017.

Ritchie, M. E., and D. Tilman. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. Ecology 76:2648–2655.

Ruess, R. W., J. M. McFarland, L. M. Trummer, and J. K. Rohrs-Richey. 2009. Disease-mediated declines in N-fixation inputs by *Alnus tenuifolia* to early-successional floodplains in interior and south-central Alaska. Ecosystems 12:489–502.

Sheffer, E., S. A. Batterman, S. A. Levin, and L. O. Hedin. 2015. Biome-scale nitrogen fixation strategies selected by climatic constraints on nitrogen cycle. Nature Plants 1: 15182.

Sokolov, A. P., D. W. Kicklighter, J. M. Melillo, B. S. Felzer, C. A. Schlosser, and T. W. Cronin. 2008. Consequences of considering carbon-nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle. Journal of Climate 21:3776–3796.

Sprent, J. I. 2009. Legume nodulation: a global perspective. Wiley-Blackwell, Ames, Iowa, USA.

Sullivan, B. W., et al. 2014. Spatially robust estimates of biological nitrogen (N) fixation imply substantial human alteration of the tropical N cycle. Proceedings of the National Academy of Sciences USA 111:8101–8106.

ter Steege, H., et al. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443:444–447.

Thornton, P. E., J.-F. Lamarque, N. A. Rosenbloom, and N. M. Mahowald. 2007. Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. Global Biogeochemical Cycles 21:GB4018.

Uliassi, D. D., and R. W. Ruess. 2002. Limitations to symbiotic nitrogen fixation in primary succession on the Tanana River floodplain. Ecology 83:88–103.

Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285–298.

Vitousek, P. M., and J. S. Denslow. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. Journal of Ecology 74:1167–1178.

Vitousek, P. M., and H. Farrington. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry 37:63–75.

Vitousek, P. M., and C. B. Field. 1999. Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. Biogeochemistry 46:179–202.

Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry 13:87–115.

Vitousek, P. M., and R. L. Sanford. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics 17:137–167.

Vitousek, P. M., et al. 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57: 1–45.

Vitousek, P. M., D. N. L. Menge, S. C. Reed, and C. C. Cleveland. 2013. Biological nitrogen fixation: rates, patterns and ecological controls in terrestrial ecosystems. Philosophical Transactions of the Royal Society B 368:20130119.

Wang, Y.-P., B. Z. Houlton, and C. B. Field. 2007. A model of biogeochemical cycles of carbon, nitrogen, and phosphorus including symbiotic nitrogen fixation and phosphatase production. Global Biogeochemical Cycles 21:GB1018.

Wårlind, D., B. Smith, T. Hickler, and A. Ameth. 2014. Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model. Biogeosciences 11:6131–6146.

Wieder, W. R., C. C. Cleveland, D. M. Lawrence, and G. B. Bonan. 2015. Effects of model structural uncertainty on carbon cycle projections: biological nitrogen fixation as a case study. Environmental Research Letters 10:044016.

Wolf, A. A., J. L. Funk, and D. N. L. Menge. 2017. The symbionts made me do it: legumes are not hardwired for high nitrogen concentrations but incorporate more nitrogen when inoculated. New Phytologist 213:690–699.

Wright, J. J., et al. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616–1625.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2034/suppinfo