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Symbiotic nitrogen fixation in trees: patterns, controls and ecosystem consequences

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Symbiotic nitrogen fixation (SNF) represents the largest natural input of bioavailable nitrogen into the biosphere, impacting key processes spanning from local community dynamics to global patterns of nutrient limitation and primary productivity. While research on SNF historically focused largely on herbaceous and agricultural species, the past two decades have seen major advances in our understanding of SNF by tree species in forest and savanna communities. This has included important developments in the mathematical theory of SNF in forest ecosystems, experimental work on the regulators of tree SNF, broad observational analyses of tree N-fixer abundance patterns and increasingly process-based incorporation of tree SNF into ecosystem models. This review synthesizes recent work on the local and global patterns, environmental drivers and community and ecosystem effects of nitrogen-fixing trees in natural ecosystems. By better understanding the drivers and consequences of SNF in forests, this review aims to shed light on the future of this critical process and its role in forest functioning under changing climate, nutrient cycling and land use.

Keywords: actinorhizal, *Frankia*, legume, nodule, rhizobia, rosids.

Introduction

Symbiotic nitrogen fixation (SNF)—the association between some vascular plants and nitrogen (N)-fixing bacteria that converts N_2 gas into bioavailable N—represents the primary source of N in many forests and has important impacts on individual, community and ecosystem N dynamics (Cleveland et al. 1999, Vitousek et al. 2013, Davies-Barnard and Friedlingstein 2020). Thousands of species of trees and shrubs occupying a wide range of ecological niches can engage in SNF (Box 1, Table 1), providing critical N inputs into forests and savannas where they occur. Yet, in many of these ecosystems, the most notable pattern of N-fixing trees is their relative absence, raising questions of why N-fixing trees and shrubs are not more abundant (particularly in N-limited ecosystems) and why their SNF activity often does not relieve N limitation (Vitousek and Howarth 1991, Menge et al. 2017*a*). These questions underpin long-standing paradoxes in the literature on SNF in forest ecosystems (Hedin et al. 2009, Reed 2017) that can only be resolved through a comprehensive understanding of the patterns and regulators of tree SNF at scales ranging from molecular to ecosystem. The goal of this synthesis is to progress toward just such an understanding.

Box 1 Assigning nitrogen fixation status to plant species

Which plant species have the capacity to form nodulating, nitrogen-fixing symbioses? This conceptually straightforward question is notoriously challenging to answer because (i) the list of plant species with the genetic capacity to engage in SNF is large (e.g., Werner et al. 2014), and (ii) confirming the nodulation capacity of a species can be highly susceptible to false negatives. That is, sampling an individual of a species and finding no nitrogen-fixing nodules does not guarantee that the species itself lacks the capacity to form nodules. The current approach to this challenge has been to establish and refine lists of confirmed nodulating species, but due to the issue of false negatives, these lists are understood to be underestimates of the true number of nodulating nitrogen-fixing plant species. Appendix 1 presents a concatenation of several species-level lists of confirmed N fixers, including > 7000 species across 14 families (Table 1). While the TRY global plant trait database (Kattge et al. 2019) provides data on N fixation capacity (listing 8877 N-fixing species), this list currently includes many non-nodulating species (e.g., several *Acer* species) and so should be approached with caution. The list in Appendix 1 also provides information on the dominant growth habit for >4500 species, including 2858 tree and shrub N fixers. While this list and others provide information on confirmed N fixers, there are >19,000 legume species and 12,000 species in the orders that contain actinorhizal fixers (Ardley and Sprent 2021), highlighting that these lists are relatively small subsets of the potential list of actual nodulating N fixers. Other approaches of using genus-level trends in nodulation (e.g., Menge, Batterman, Liao et al. 2017) or foliar N concentration data as an indicator of SNF capacity (Doby et al. 2024) allow researchers to estimate the N-fixation capacity of the many likely, but as yet unconfirmed, N fixers.

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Table 1. Number of genera with confirmed N-fixing species and the number of confirmed N-fixing species in each family listed in Appendix 1. Species in the Fabaceae and one genus (*Parasponia*) in the Cannabaceae form nodules with rhizobia bacteria. All other species form nodules with *Frankia*.

Family	Genera containing N-fixers	Confirmed N-fixing species
Betulaceae	1	25
Cannabaceae	4	10
Casuarinaceae	3	15
Coriariaceae	1	12
Elaeagnaceae	3	14
Fabaceae	664	4263
Lembophyllaceae	2	1
Myricaceae	3	12
Nelumbonaceae	1	1
Rhamnaceae	4	31
Rosaceae	3	8
Rubiaceae	1	1
Urticaceae	1	1
Zygophyllaceae	4	7

The process of SNF relies on a fundamental resource exchange between the plant host and bacterial symbiont. Bacteria housed inside specialized plant structures called nodules convert N_2 gas into ammonia (NH_3), which the host plant takes up and uses as a N source for a wide suite of biological functions. In exchange for this N source, the plant provides a stable low-oxygen growth environment within the nodule and a labile carbohydrate energy source (derived from photosynthates) to the bacteria (Mylona et al. 1995). For the plant host, SNF can represent a critical N source, supplementing N uptake from the soil to meet plant N demands. For the bacteria, while they can survive in a free-living state in the bulk soil, the conditions within a host nodule allow the bacteria to divide and differentiate into reproductive cells that serve as the primary mode for bacterial population growth, which are eventually released back into the soil following nodule senescence (Oono et al. 2009, Denison and Kiers 2011, Komatsu and Simms 2020). Thus, this partnership facilitates the primary mode of reproduction for the bacteria and provides one of the most important elements (N) supporting biological function in the plant.

In trees and shrubs, two broad groups of plant–bacterial partnerships engage in SNF. Rhizobial SNF is carried out primarily by plants in the Fabaceae family that partner with rhizobia N-fixing bacteria, while actinorhizal SNF is conducted by various plant species in the Rosid I clade that partner with N-fixing bacteria in the genus *Frankia*. Rhizobial N fixers are by far the more prolific group, both in species richness of plant hosts (as many as 17,000 legume species may engage in SNF vs 230 actinorhizal N-fixing species) and global abundance (Ardley and Sprent 2021, Tamme et al. 2021). These two partnerships share the same basic resource exchange described above but differ markedly in their ecology and biogeographic patterns.

Ecologically, actinorhizal N fixers are almost exclusively trees and shrubs, while rhizobial N fixers also contain many vine and herbaceous species (Appendix 1). Historically, these two groups were also thought to differ in their SNF strategies. The paradigm through much of the late 20th century posited that actinorhizal N fixers exhibit an 'obligate' SNF strategy where the plant fixes N at relatively constant rates per unit plant biomass regardless of environmental N availability (Binkley et al. 1992). Alternatively, rhizobial N fixers were assumed to have a 'facultative' SNF strategy, where the plant actively regulates SNF rates based on environmental conditions—again, often viewed as environmental N availability (Menge et al. 2009, Barron et al. 2011, Bauters et al. 2016). Recently, this obligate–facultative dichotomy has been increasingly viewed as a spectrum of SNF regulation ability, with evidence that at least some actinorhizal N fixers can actively regulate SNF in response to environmental conditions such as temperature (Bytnerowicz et al. 2022) and soil N availability (Menge et al. 2023), and rhizobial N fixers can exhibit a range of SNF regulation abilities (Menge et al. 2015, 2023).

The following review seeks to synthesize current knowledge on the ecological role of woody symbiotic N-fixing plants in forest and savanna ecosystems. This includes discussing the broad phylogenetic and biogeographic patterns of woody N fixers, the ecological factors that regulate their abundances and SNF rates, the ecological impacts that N fixers have on forest and savanna ecosystems and the current understanding of how woody SNF is likely to respond to global change. A set of priorities for future research on woody SNF is then presented with the hope of guiding further discovery on woody SNF in the coming decades.

Phylogenetic and biogeographic patterns of N-fixing trees and shrubs

Important work over the past two decades has continued to clarify the evolutionary history of N-fixing angiosperms and the emergence and loss of the N-fixing trait. All N-fixing angiosperms belong to one of four orders (Cucurbitales, Fabales, Fagales and Rosales) in the Rosid I clade (Doyle 2011, Soltis et al. 1995). How many times the N-fixing trait has arisen within this clade, however, remains actively debated. Currently, the most commonly held view is that a single, cryptic, evolutionary precursor evolved in this clade > 100 MYA, creating the genetic capacity for nodulating symbioses (Werner et al. 2014, Kates et al. 2024). Within this framework, estimates for the number of independent gains and losses of nodulating N-fixing symbioses vary, but are commonly estimated at 8–16 independent gains and 10 independent losses (Werner et al. 2014, Kates et al. 2024), with all of the losses of nodulating SNF happening in the legume–rhizobia symbiosis (Kates et al. 2024). Within the actinorhizal N fixers, there is consensus that nodulating symbioses have evolved nine independent times (Kates et al. 2024), which Li et al. (2015) suggest were evolutionary gains associated with geologic time periods of warm temperatures and high CO_2 concentrations. However, an alternative view is that the actual trait of nodulating SNF arose only once (negating the need for a cryptic evolutionary precursor to explain the monophyly of SNF within the Rosid I) and has undergone parallel losses creating the nonfixing groups within the Rosid I clade (van Velzen et al. 2019). Continued improvement of phylogenomic data and the fossil record holds promise for resolving the evolutionary origins of SNF in coming decades.

Within the dominant N-fixing family, Fabaceae (legumes), recent molecular data has revised the historical three subfamilies (Caesalpinioideae, Mimosoideae and Papilionoideae) into six distinct subfamilies (a revised Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae, Duparquetioideae and revised Papilionoideae), with the previous subfamily Mimosoideae now occupying a distinct group within the Caesalpinioideae (Legume Phylogeny Working Group and Hughes 2017). Whereas each of the three historic subfamilies contained a mix of N-fixing and nonfixing species, four of the new subfamilies (Cercidoideae, Detarioideae, Dialioideae and Duparquetioideae) are entirely nonfixing, with the revised Caesalpinioideae and Papilionoideae containing both fixing and nonfixing clades (Sprent et al. 2017). These major shifts in legume phylogeny are largely due to shifting the phylogeny from one based on floral characteristics to one based on chloroplast genes, but additional characteristics such as nodule structure and infection process are important tools for resolving several revised subfamilies (Sprent et al. 2017).

The biogeographic patterns of N-fixing trees and shrubs have received substantial attention for their importance in understanding both the ecology and the evolutionary history of SNF in forests and savannas. Much of this work focuses on the dramatic decline in N-fixing tree relative abundance moving poleward from the equator (Menge et al. 2014, Steidinger et al. 2019) (but see Adams et al. 2010). Woody N fixers are much more diverse in tropical forests than at high latitudes (Tamme et al. 2021), which was originally invoked as a potential explanation for declining abundances moving poleward. However, revisions to legume biogeographic history suggest this clade originated in high-latitude Laurasia, dispersing southward to tropical latitudes and subsequently diversifying (Doyle and Luckow 2003, Schrire et al. 2005), suggesting sufficient evolutionary time to diversify in high-latitude forests if this were ecologically beneficial. Indeed, Menge and Crews (2016) evaluated several hypotheses for evolutionary constraints to the diversification of N-fixing trees at high latitudes and found that the evolutionary opportunity has existed for many more N-fixing tree species to evolve at high latitudes than currently exist, suggesting ecological constraints largely drive low N-fixer abundances near the poles. This was later corroborated by analyses showing that while N-fixing trees are less abundant at high latitudes, they do not make up a smaller proportion of the total tree species pool in high-latitude forests than in the tropics (Menge et al. 2017*b*).

One of the most distinct ways that phylogenetic and biogeographic patterns interact in N-fixing trees is the latitudinal shift from rhizobial N-fixing trees dominating tropical latitudes (ter Steege et al. 2006) to actinorhizal N-fixing species dominating higher-latitude forests (Menge et al. 2014, Tamme et al. 2021). While previous theoretical work suggested the purported difference in the ability to regulate SNF (the idea that rhizobial N fixers have the ability to facultatively regulate SNF while actinorhizal N fixers obligately fix N at constant rates) could drive this latitudinal tradeoff in dominant taxa (Menge et al. 2009, Sheffer et al. 2015), more recent experimental work shows similar abilities of temperate and tropical rhizobial and actinorhizal N fixers to regulate SNF (Menge et al. 2023), suggesting that some other characteristic(s) of actinorhizal N fixers explain their relative dominance at high latitudes. While not the focus of this review, it is also important to note that many nonwoody rhizobial N-fixing species are abundant at latitudes as high as the Arctic circle (Sprent et al. 2013, Sprent et al. 2017), underscoring the fact that the trait of SNF itself can be successful in high-latitude ecosystems.

The overall lack of support for evolutionary/phylogenetic explanations for the latitudinal pattern of N-fixing trees strongly suggests that ecological forces such as climate and soil nutrients drive the latitudinal decline in N-fixer abundances and the shift in dominance from rhizobial N fixers in the tropics to actinorhizal N fixers in temperate and boreal forests (Houlton et al. 2008, Sheffer et al. 2015, Menge et al. 2017*a*, Steidinger et al. 2019). These ecological controls are described in detail below. Importantly, the vast majority of data supporting these biogeographic patterns comes from the Americas (Menge et al. 2014, Steidinger et al. 2019), and latitudinal patterns do not seem to be as strong in the African and Asian tropics (Adams et al. 2010, Menge et al. 2019), but many more data are needed in these regions. Moreover, while the presence of many common actinorhizal N fixers (e.g., in the genus *Alnus*) in high-latitude Eurasia suggests that the latitudinal shift from rhizobial to actinorhizal N fixers is a global phenomenon, these patterns have never been formally assessed outside of the Americas.

Ecological controls of N-fixer abundance and SNF rates

Given the importance of SNF to the terrestrial N cycle, understanding the factors that regulate SNF is critical for modeling current N cycling and how it will shift under changing environmental conditions. Nitrogen inputs into ecosystems through SNF are the product of individual SNF rates and the abundance of N fixers across the landscape (Menge et al. 2017*a*), and these two components of SNF patterns can respond separately to ecological factors (Figure 1). That is, first principles would suggest that ecological conditions that maximize SNF rates of an individual plant should also be conditions that make N fixers relatively abundant in plant communities, but this assumption is often not borne out in nature (e.g., Vitousek and Howarth 1991). In many cases, N fixers exhibit high SNF rates (suggesting the SNF trait is advantageous) but are rare across the landscape (suggesting a separate control on their abundances), while in other cases, putative N fixers can be quite common but rarely engage in SNF (Menge et al. 2017*a*). This common disconnect between SNF rates and N-fixer abundances highlights the often-separate regulation of SNF at the individual and community scales.

Potential explanations for how SNF might be regulated differently at the individual and community scales include: (i) individual SNF being imperfectly regulated to match plant N demand such that SNF rates remain high when SNF is not advantageous for the plant (Menge et al. 2008); (ii) traits common to N fixers that are not directly tied to SNF (Adams et al. 2016, Gei et al. 2018, Bytnerowicz et al. 2022; Box 2, Figure 2) creating competitive advantages or disadvantages under certain conditions and/or; (iii) N-fixing bacteria inducing over- or under-fixation in plants creating a mismatch between actual SNF rates and those optimal for N-fixing plants (e.g., Taylor and Komatsu 2024). Given the complexity of SNF regulation, the following discussion of ecological controls on SNF is structured around key concepts of the costs and benefits of SNF for individual N fixers, abiotic regulators of SNF and biotic regulators of SNF.

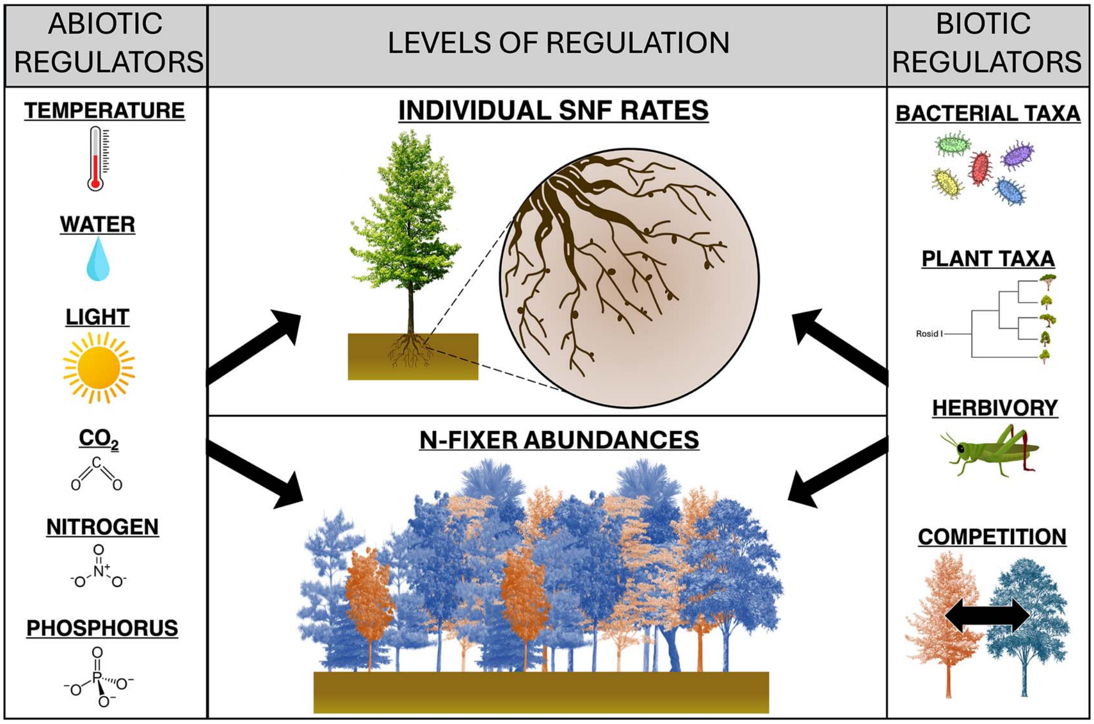

Figure 1. Environmental controls of forest symbiotic N fixation (SNF). SNF can be regulated by abiotic factors such as temperature, water, light, atmospheric CO_2, soil N and soil P. Biotic regulators of SNF include the identity and diversity of N-fixing bacteria, the identity of the N-fixing plant, herbivory of N fixers and competition with nonfixing plants. Both abiotic and biotic regulators can influence the SNF rates of individual N fixers and the relative abundances of N-fixing (red trees in bottom center) versus nonfixing (blue trees in bottom center) trees.

Box 2 Unique traits of nitrogen-fixing plants

While the capacity to fix N is the hallmark trait of nitrogen-fixing plant species, there is growing interest in the many physical and physiological ways that N-fixing plants differ systematically from nonfixing plants. Leaf N concentrations are higher, on average, in N fixers than in nonfixers (Fyllas et al. 2009, Adams et al. 2016, Bytnerowicz et al. 2023), which leads to other physiological differences such as higher water use efficiency (Adams et al. 2016, Bytnerowicz et al. 2023). This led Adams et al. (2016) to argue that legumes (the dominant N-fixing family) are fundamentally different physiologically than non-legumes. Subsequent re-analysis of Adams' data shows that traits like photosynthesis and water use efficiency scale with leaf N in the same manner between N fixers and non-fixers, and that the fundamental difference between the groups largely lies in the differences between leaf N and leaf mass per area (Bytnerowicz et al. 2023).

In fact, N fixers may systematically differ from nonfixers in several additional traits. Figure 2 illustrates bootstrapped comparisons (to account for differences in the number of N-fixing and nonfixing species) of key physical and physiological traits represented in the TRY global plant trait database (Kattge et al. 2019). In addition to containing higher foliar N concentrations, N fixers also have more N in their stems, fine roots and absorptive roots (a subset of fine roots) (Figure 2). Interestingly, data available in TRY shows that photosynthetic rates per unit leaf area are actually lower for N fixers than nonfixers. One possible explanation for this is that many N fixers occupy relatively harsh ecological niches (e.g., sites that are arid, have poor soils, etc.), and thus exhibit more conservative photosynthetic rates, on average. In this way, the trait of SNF may be viewed as either a means to grow quickly in competitive environments (leading one to expect high photosynthetic rates for N fixers) or as a means to tolerate harsh ecological conditions (creating the expectation for low N-fixer photosynthetic rates).

Although first principles might suggest that N fixers would construct their root systems differently than nonfixers (e.g., reducing allocation to roots and altering specific root length based on different demands for root N, water and P uptake), data from TRY do not indicate systematic differences in how N fixers and nonfixers construct their root systems (other than the production of nodules).

These analyses are intended to serve as examples of the insight that can be gained from leveraging large publicly available datasets on plant traits to better understand the ecophysiological differences between N-fixing and nonfixing species. Analyses like these could provide key insights into the factors that determine when SNF is advantageous for an individual N-fixer and the conditions that promote N-fixer abundances (even when SNF is not upregulated).

Costs and benefits of SNF for N fixers

From the plant's perspective, the fundamental tradeoff of SNF is a carbon (C) cost provided to N-fixing bacteria in exchange

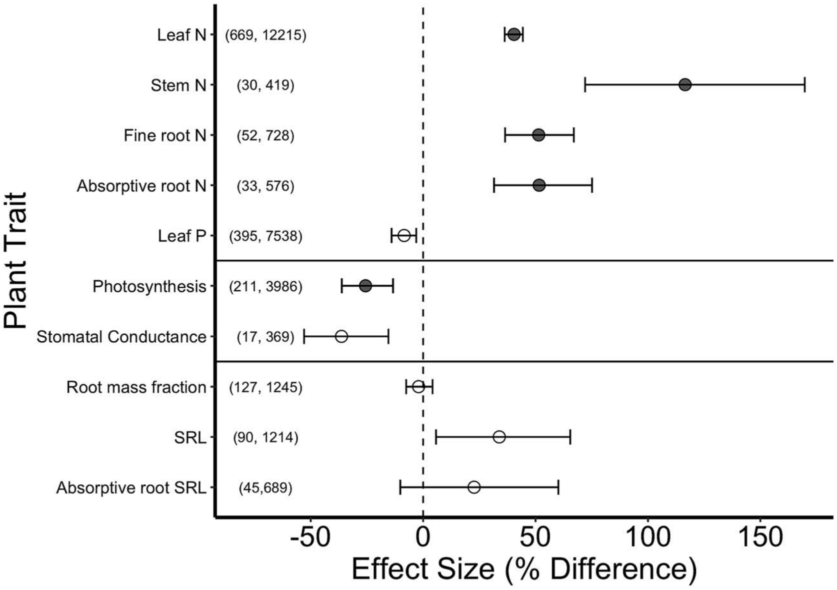

Figure 2. Differences in chemical, physiological and structural traits between nitrogen-fixing and nonfixing. Effect sizes are the percent difference between N-fixing and nonfixing species (positive values indicate N-fixers exhibit higher values for that trait). Comparisons are bootstrapped to control for unequal sample sizes between N-fixing and nonfixing species. Numbers in parentheses indicate the number of N-fixing and nonfixing species, respectively, used in each comparison. Solid points indicate bootstrapped *t*-tests where $P < 0.05$. Error bars represent 95% confidence interval of 1000 bootstrapped effect size estimates. Details of analyses can be found in Appendix 2.

for the N benefit of fixation. The C costs of SNF are typically categorized as structural (i.e., construction and maintenance of nodules) and nonstructural (i.e., labile C supporting the metabolism of bacterial endosymbionts). While difficult to measure in the field, structural C allocation to nodules is a small portion of belowground biomass for most trees (e.g., Taylor and Menge 2021), and this structural cost is typically assumed to be a small component of the total energetic costs of SNF (Gutschick 1981, Rastetter et al. 2001). That said, rare estimates of nodule turnover suggest that the structural costs of nodule production may be incurred several times per year (Nygren and Ramirez 1995, Srivastava and Ambasht 1995), highlighting the need for better data on nodule lifespan to estimate the realized structural cost of nodules over time. Labile C costs of SNF typically range from 8 to 12 g of glucose per g of N fixed, which is higher than other methods of N acquisition (i.e., uptake via roots and mycorrhizae) under all but the most severely N-limited conditions (Gutschick 1981). In a C economy framework, the relative value of these C costs depends heavily on the photosynthetic capacity of the plant, which is driven by a suite of environmental factors (see section on abiotic controls below). In addition to the structural and nonstructural C costs, it has been argued that the ability to fix N must represent some ‘intrinsic costs’ to N fixers, otherwise all plants should have evolved the ability to fix N but only do so under advantageous conditions. These intrinsic costs could include the additional genetic burden of N-fixing genes, physiologic costs of plasticity in the SNF trait (van Kleunen and Fischer 2005), or the cost of requiring specific environmental conditions for SNF (Rastetter et al. 2001), but the effect of these costs on N-fixer performance has never been directly quantified.

The relative value of N benefits from SNF for the host plant is heavily dependent on environmental conditions—particularly those that determine N availability and N demand for the plant. The high per-capita C costs of SNF (Gutschick 1981) suggest that SNF should be a poor N-acquisition strategy when ecosystem N is abundant. However, in conditions where soil N availability is scarce, the relative value of fixed N can be high as the per-capita C costs of N uptake from the soil become increasingly high. This can make SNF an advantageous strategy in extremely N-limited conditions and makes N fixers relatively common in recently disturbed, N-poor soils (e.g., Chaer et al. 2011). Additional important indirect benefits of the N acquired via SNF exist, including improved water use efficiency, herbivory defense and phosphorus (P) acquisition. Interestingly, these benefits are not exclusively tied to how much N is fixed via SNF. Evidence from herbaceous legumes shows that increases in foliar N concentrations (which can affect photosynthetic rates and water use efficiency) can exceed the additional N provided by SNF, suggesting more fundamental physiological changes can be induced by the N-fixing symbioses (Wolf et al. 2017), but what drives these changes is not well understood.

Abiotic controls of SNF

The majority of research on the ecological drivers of SNF, particularly in woody plants, has focused on how abiotic conditions impact SNF rates and N-fixer abundances. Of the many potential abiotic regulators, the most well-studied are soil N, soil P, water, temperature and light. The literature on these abiotic controls is large, but recent work has demonstrated the following broad conclusions for each of these abiotic SNF regulators.

Soil N serves as the most logical regulator of SNF, as uptake of soil N via roots and mycorrhizae is the direct alternative to SNF for N acquisition. Under this framework, higher soil N availability should downregulate individual SNF and reduce N-fixer abundances as SNF becomes a less advantageous strategy. Indeed, many N fertilization studies support the expectation that increasing soil N downregulates individual

SNF rates (Zheng et al. 2019), but several studies demonstrate that other environmental factors such as light, CO_2 and soil P can mediate the effects of N fertilization under certain conditions (Batterman et al. 2013*b*, Taylor and Menge 2018, Nasto et al. 2019, Ottinger et al. 2023). How soil N affects woody N-fixer abundances is substantially more complex. Because few fertilization studies have been conducted in forests for sufficient lengths to see dramatic shifts in tree communities, we lack direct experimental evidence of N fertilization effects on N-fixer abundances. Observationally, much work has focused on the latitudinal pattern that N-fixing trees are more abundant in the N-rich tropics and largely absent from the N-limited temperate and boreal regions (see above section on biogeographic patterns)—a direct contradiction to the expectation that N fixers should be more abundant in N-limited environments where SNF provides the largest competitive advantage (Hedin et al. 2009). Qualitatively, these biogeographic patterns support the experimental evidence that other environmental factors such as light, temperature, water and non-N nutrients can be strong drivers of SNF, creating seemingly paradoxical patterns of N-fixer abundances and N limitation (Houlton et al. 2008).

In addition to soil N, soil P availability could regulate tree SNF, as N fixers could use N from SNF to produce phosphatase enzymes to acquire soil P and relieve P limitation, particularly in tropical forests where N-fixing trees are relatively common and P limitation is also common (Du et al. 2020). Indeed, several studies have shown increased phosphatase activity associated with N-fixing legumes (Gei and Powers 2013, Batterman et al. 2013*b*, Nasto et al. 2014, 2019), an effect that has been used in theoretical models to explain N-fixer abundances and SNF in P-limited tropical forests (Wang et al. 2007, Houlton et al. 2008). Png et al. (2017) found increased phosphatase under Australian legume N fixers, which was most prominent in severely P-limited soils, but that actinorhizal N fixers do not exhibit increased phosphatase. However, direct evidence for N fixers employing so-called ‘N for P’ trading is rare, with most studies determining that while some N fixers do rely on high phosphatase production for P acquisition, others do not and that this is a species-specific trait that is not directly related to SNF (Png et al. 2017, Batterman et al. 2018, Soper et al. 2019). Maybe the most direct evidence for this is that N-for-P trading should result in a negative correlation between P availability and SNF, but most studies find increases in SNF when plants are fertilized with P (Crews 1993, Uliassi and Ruess 2002, Batterman et al. 2013*b*). This positive response of SNF to P fertilization is also supported by global meta-analysis, which shows an 85% stimulation of SNF under P fertilization (Zheng et al. 2019). Thus, the current evidence suggests that P limitation of SNF is relatively common in P-limited conditions, but that SNF as a mechanism to overcome P limitation is a species-specific phenomenon.

High light availability drives higher photosynthetic C assimilation, providing more C for the plant to allocate to SNF and also increasing plant N demand—both of which should increase individual SNF. Experimental and observational work in both tropical and temperate trees shows that high light conditions can substantially increase SNF, and that the impact of light is strongest under low soil N conditions (Myster 2006, Barron et al. 2011, Taylor and Menge 2018, 2021, McCulloch and Porder 2021, Ottinger et al. 2023, Schmidt et al. 2023). While it is possible that high levels of solar radiation at the equator declining toward the poles could help explain the latitudinal decline in N-fixer abundances, this idea has never been explicitly tested. However, high light availability is likely an important contributor to high N-fixer abundances in early successional stages of both tropical and temperate forest regeneration (Batterman et al. 2013*a*, Bauters et al. 2016, Liao and Menge 2016, Winbourne et al. 2018, Taylor et al. 2019).

Temperature can have direct and indirect effects on SNF, all of which operate to increase SNF at warmer temperatures up to an optimum that is at the high end of ecologically relevant temperatures. Temperature directly impacts SNF by influencing the enzymatic efficiency of the nitrogenase enzyme that drives SNF (Waughman 1977). Recent experimental work has shown that SNF optimizes at 29–37 °C air temperature for a variety of woody N fixers, and that SNF’s temperature optimum acclimates to growing conditions for tropical but not temperate species (Bytnerowicz et al. 2022). Lab studies of soil temperature manipulation have also shown substantial inhibition of SNF by *Alnus* shrubs at low soil temperatures (Anderson and Markham 2021). These data suggest that in most environments, warmer temperatures increase SNF efficiency, but temperature response curves are often asymmetric, indicating that SNF drops off quickly at temperatures above its optimum (Bytnerowicz et al. 2022).

Temperature also affects SNF by influencing photosynthetic rates, and thus, N demands. Temperature optima for photosynthesis are often slightly lower than for SNF (Bytnerowicz et al. 2022), suggesting that high temperatures will restrict plant C supply to SNF before direct temperature inhibition of nitrogenase (Aranjuelo et al. 2015). At broad geographic scales, inhibition of SNF at cold temperatures has been used to explain the paucity of N-fixing trees at N-limited high latitudes (Houlton et al. 2008). While the parsimony of this explanation is attractive, the fact that other N-fixing functional groups such as N-fixing herbs, shrubs and aquatic N fixers have many successful taxa in high-latitude cold environments (Sprent et al. 2013, 2017, Li et al. 2022) suggests that direct temperature limitation on nitrogenase activity is not the only explanation for the latitudinal gradient in N-fixing trees. However, game theoretical analyses show that the effect of cold temperatures slowing soil C decomposition and creating high soil C:N at high latitudes can also drive latitudinal shifts between facultative SNF in tropical forests and obligate SNF in extra-tropical forests (Sheffer et al. 2015). Thus, temperature likely plays direct (regulation of nitrogenase efficiency) and indirect (e.g., influencing ecosystem properties such as C and N cycling, plant growth rates and N demand) roles in influencing the latitudinal distribution of N-fixing trees and the dominant SNF regulation strategy.

Because water availability influences multiple aspects of plant physiology and soil resource acquisition, it can have particularly strong and complex impacts on SNF and N-fixer abundances. At the individual scale, SNF can be strongly downregulated under extremely dry conditions (Dovrat et al. 2018, Dovrat and Sheffer 2019) or frequent drought cycles (Minucci et al. 2017). Moderately dry conditions could increase SNF via at least two potential mechanisms—high foliar N from upregulated SNF makes N fixers more water-use efficient (Adams et al. 2016, Bytnerowicz et al. 2023), and dry soils reduce bulk flow of inorganic N to roots creating the perception of N limitation regardless of how much N is actually present in the soil (Wurzburger and Miniat 2014).

However, if wet conditions are optimal for plant growth, this could increase N demand and upregulate SNF. At the highest end of the precipitation spectrum, extremely wet conditions could induce sufficient N leaching from the soil to create N limitation and increase SNF. At broad scales, there is evidence that within the precipitation range that supports forests (>500 mm year^{-1}), drier climates often hold more N fixers (Gei et al. 2018, Steidinger et al. 2019, Staccone et al. 2020), likely driven largely by the N fixers' high water-use efficiency (Adams et al. 2016, Bytnerowicz et al. 2023). However, the most common N-fixing tree in North America, *Robinia psuedoacacia*, can be disproportionately disadvantaged by dry soils (Minucci et al. 2019). Together, the current literature suggests that moderately (but not extremely) dry conditions often increase individual SNF rates and N-fixer abundances, but that notable exceptions exist for these patterns.

Biotic controls of SNF

In addition to the abiotic drivers discussed above, several key biotic factors can regulate individual SNF rates and N-fixer abundances, although these factors have received relatively little empirical attention (particularly in forest systems). Of the biotic factors that likely regulate SNF, taxonomy (of both plant and bacteria), competition and herbivory stand out as particularly important factors.

Nitrogen-fixing partnerships vary substantially in their ability and efficiency to fix N, which strongly suggests that the taxonomic identities of the N-fixing plant and bacteria present are important drivers of ecosystem SNF. Indeed, Wurzburger and Hedin (2016) found that tree species identity was the most important factor determining nodulation and SNF in a lowland Panamanian forest, and SNF ranged from 2 to 71% N derived from fixation in a set of co-occurring N fixers in Namibia (Schulze et al. 1991). Substantial differences in how N-fixing species regulate SNF in response to environmental factors (Batterman et al. 2013*a*, Menge et al. 2015, 2023, Batterman et al. 2018, Bytnerowicz et al. 2022) also underscore the importance of N-fixer taxonomy.

In addition to the important effects of N-fixing plant species, substantial work shows that different N-fixing bacterial taxa affect plant growth and fix N at different rates and efficiencies (Batzli et al. 1992, Cordero et al. 2016, Moura et al. 2020). This means that the availability and diversity of prospective bacterial symbionts in the soil can have important implications for SNF rates (Taylor et al. 2020). More diverse communities of rhizobia in the soil have been experimentally shown to increase N-fixer growth rates and SNF (Taylor and Komatsu 2024), suggesting that the diversity of both N-fixing trees and their bacterial symbionts are important regulators of N inputs into natural and managed forests (Moura et al. 2020, Taylor et al. 2020).

Interactions with neighboring plants also have the potential to regulate SNF in forests. At broad scales, competition with nonfixing trees eventually excludes most tree SNF from mature temperate and boreal forests (Liao and Menge 2016) but does not have this effect in many tropical forests (Batterman et al. 2013*a*, Menge and Chazdon 2016, Gei et al. 2018). At the individual scale, increased competition from neighboring trees could induce N fixers to upregulate SNF if competition induces increased N limitation, or N fixers could downregulate SNF as a means to reduce energetic costs in a more competitive environment. Of the few studies to evaluate this in nonagricultural N fixers, both show that the presence of nonfixing competitors induces downregulation of SNF (Taylor and Menge 2021, Dagan et al. 2023). How the individual-scale effects of neighboring competitors on N-fixer SNF impact the geographic and successional patterns of N-fixer abundances remains an open question.

Finally, it is important to consider top-down impacts of herbivory on SNF and N-fixer abundances. It has long been postulated that N-fixer abundances are constrained, in part, by herbivores preferentially feeding on the N-rich leaves of N fixers (Mattson 1980, Vitousek and Howarth 1991, Menge et al. 2008, Kurokawa et al. 2010). Alternatively, N fixers could use excess leaf N to produce defensive compounds that deter herbivores (Mattson 1980, Menge et al. 2008). To date, surprisingly few empirical studies have directly evaluated whether N-fixing trees receive more herbivory than neighboring nonfixers and what mechanisms drive this pattern. While not all studies show increased herbivory for N-fixing trees (Taylor and Ostrowsky 2019), by far the most comprehensive study on herbivory costs to N fixers indicates that lowland tropical N-fixing trees receive significantly more herbivory and incur a disproportionate C cost of this herbivory relative to nonfixing trees (Barker et al. 2022). The majority of studies on N-fixer herbivory have focused on invertebrate herbivores, but evidence for ungulate browsers preferentially feeding on N-fixing species also exists and has been cited as an important link between large-bodied consumers and ecosystem N cycling (Knops et al. 2000). How herbivory regulates individual SNF rates (and vice versa) and what role herbivory plays in determining N-fixer abundance patterns are important next steps in understanding the ecology of N-fixing trees.

Ecological effects of tree symbiotic N fixation

Given their unique ability to convert N_2 into bioavailable N, N-fixing trees are one of the most important functional groups in many forest and savanna communities, commonly providing N inputs of 1.4–11 kg N ha^{-1} year^{-1} in temperate forests (Staccone et al. 2020, Wurzburger et al. 2021) and 2–30 kg N ha^{-1} year^{-1} in tropical forests (Batterman et al. 2013*a*, Winbourne et al. 2018, Brookshire et al. 2019, Taylor et al. 2019). Even in ecosystems where N-fixer abundances are low in mature forests, N fixers often play important transient roles during forest succession. While most work on the ecological impacts of N fixers focuses on their contributions to N cycling, several additional ecological effects of N-fixing trees (described below) can also be important to forest function.

Clearly, N-fixing trees play an important role in bringing N into forests—particularly early successional forests. Much ecosystem theory (Vitousek and Field 1999, Rastetter et al. 2001, Menge et al. 2008, Fisher et al. 2010, Levy-Varon et al. 2019) and empirical work (Batterman et al. 2013*a*, Sullivan et al. 2014, Winbourne et al. 2018, Taylor et al. 2019) demonstrate the particularly critical role that N-fixing trees play in N cycle recovery of regenerating forests and supporting incremental biomass gains in mature forests (Brookshire et al. 2019). There is also direct isotopic evidence (from boreal peatlands) that fixed N from SNF enhances the tissue N concentrations of neighboring plants (Zhang et al. 2024), providing a mechanistic link between SNF and benefits to neighboring plants.

Despite well-established impacts of SNF on ecosystem N availability, it is often challenging to link these N inputs directly to forest growth rates. One approach to this challenge is to calculate or model total N demand of forest growth and estimate forest-wide SNF rates for the same forest to calculate the portion of the growing forest's N demand that is supported by SNF. This approach has provided strong evidence for N fixers facilitating forest growth, particularly in regenerating tropical forests (Batterman et al. 2013*a*, Brookshire et al. 2019, Levy-Varon et al. 2019). However, the effect of individual N fixers on the growth of neighboring trees can range from negative (Chapin et al. 2016, Taylor et al. 2017) to neutral (Lai et al. 2018, Xu et al. 2020) to positive (Minucci et al. 2019). In the most comprehensive of these assessments, Staccone et al. (2021) show that these effects vary widely over large geographic scales (coterminous USA) and that N fixers tend to facilitate neighbors most in scenarios where the N fixer itself should be less competitive. Meta-analysis of studies comparing plots with and without N fixers also shows highly variable effects of N fixers on nonfixer growth, but that N fixers promote nonfixer growth more often than not (Ortiz and Wolf 2024). Overall, the balance between the benefits of fixed N and the competitive influence of N fixers on neighboring plants is highly context dependent.

In addition to the direct effects of N-fixing trees on forest N cycling and biomass, N fixers can have several important but underrecognized indirect effects on forest ecosystems. N fixers often mediate important soil properties, such as acidifying the soil (Russell and Raich 2012) and increasing soil C accrual (Wang et al. 2010, Peng et al. 2020, Koutika et al. 2021, Ye et al. 2022) through changes in soil microbial communities (Binkley 2005). Nitrogen-fixing trees can also have important impacts on biotic interactions. Because the seeds of N fixers (particularly rhizobial N fixers) are disproportionately animal-dispersed (Wilcots et al. 2019), N fixers often serve as important food sources for frugivores and granivores. Nitrogen fixers can also mediate the diversity of the neighboring tree community (Ortiz and Wolf 2024)—increasing or decreasing neighborhood diversity in N-rich and N-poor sites, respectively (Xu et al. 2020). Together, these studies highlight the important ecological impacts that N-fixing trees have on both the abiotic and biotic functions of forests.

Forest SNF and global change

The sensitivity of tree SNF to many environmental factors (Ecological controls of N-fixer abundance and SNF rates) means that SNF in forests will be directly impacted by several aspects of global climate change, and the important roles that N fixers play in global forest functioning (Ecological effects of tree symbiotic N fixation) mean that changes to tree SNF will, in turn, influence the trajectory of forest C capture and climate change itself.

How is global change likely to impact forest SNF? Of the abiotic regulators of SNF described in Section 2, rising temperatures, increasing drought and increasing P deposition driven by global change should all act to increase SNF and/or N-fixer abundances. Warming temperatures should increase the enzymatic efficiency of SNF (Bytnerowicz et al. 2022), but whether N fixers as a group are more tolerant of heat stress is an open question (Slot et al. 2021). Substantial evidence suggests that N fixers are more water-use efficient (Adams et al. 2016), and thus, may increase under regimes of more frequent drought. Given the common P limitation of SNF (Zheng et al. 2019), anthropogenic increases in P availability should also increase SNF. Additional global change drivers that should also operate to increase SNF include rising CO_2 reducing C limitation of SNF (Hungate et al. 1999, Trierweiler et al. 2018, Cui et al. 2024, Yaffar et al. 2024) and increasing human land use creating more early-successional forests (Batterman et al. 2013*a*, Sullivan et al. 2014, Liao and Menge 2016, Winbourne et al. 2018, Taylor et al. 2019, Wurzburger et al. 2021).

Anthropogenic N deposition should reduce forest SNF (Zheng et al. 2019, Wurzburger et al. 2021), although whether terrestrial N availability will increase or decrease over the coming century is currently unclear (Mason et al. 2022, Cui et al. 2024). These studies suggest that individual SNF rates are likely to increase under most climate change scenarios for the coming century. At large scales, climate envelope modeling indicates that N-fixer abundances will also increase in many areas, primarily due to warming temperatures (although this work did not consider effects of rising CO_2; Liao et al. 2017).

If SNF does, indeed, increase over the coming century, how will this impact future forest function? One of the most important roles of SNF will be providing N inputs to fuel additional terrestrial C capture—an effect that is often evaluated using dynamic vegetation and Earth system models (ESMs) (Xu-Ri and Prentice 2017, Levy-Varon et al. 2019, Davies-Barnard et al. 2022). Most global models project increasing SNF over the coming century, largely due to coupling of the modeled N cycle with an increasing terrestrial C sink driving higher external N demands (Thomas et al. 2015, Xu-Ri and Prentice 2017). So, while global models rely heavily on increasing SNF to support future additional C capture, increases in SNF have historically been modeled based on coupling of N fixation to some proxy of vegetation (i.e., NPP, evapotranspiration, N limitation) rather than on mechanistic SNF responses to changing environmental conditions (Wieder et al. 2015). For example, of the 11 models in the TRENDY-N ensemble, different representations of N fixation include mechanistic environmental controls in one model, N fixation modeled as a function of vegetation N limitation in three models, N fixation tied to NPP or evapotranspiration in four models and three models where N fixation is either time invariant or used to close the model's N cycle (Kou-Giesbrecht et al. 2023). While current models predict up to an 80% increase in biological N fixation over the coming century (Davies-Barnard et al. 2022), there is wide recognition that a more mechanistic representation of N fixation is needed to accurately determine the ability of N fixation to support a growing terrestrial C sink (Stocker et al. 2016, Davies-Barnard et al. 2022, Kou-Giesbrecht et al. 2023). It is also important to note that potential increases in SNF over the coming century can also have important impacts on other ecosystem fluxes, such as N_2O emissions, which could partially counteract the climate forcings of SNF increasing terrestrial C capture (Kou-Giesbrecht and Menge 2019). Together, current evidence suggests that SNF will likely increase over the coming century, that this will create both positive and negative climate forcings, but that the dominant effect is likely to be SNF supporting additional terrestrial C capture, mitigating atmospheric CO_2 accumulation.

Unresolved questions and avenues for future research

Despite important recent work on tree SNF, much about the regulation and impacts of this process remains unresolved. Outlined below are a set of particularly important next steps in research among the myriad unanswered questions surrounding woody SNF.

- Incorporating interacting environmental regulation of SNF. Much important work has identified how individual, or occasionally, two environmental factors work to regulate SNF, but we have a poor understanding of how temperature, water, CO_2, light, soil nutrients, pH and other abiotic factors interact to produce the N-fixer abundances and SNF rates seen in nature. Given the logistical complexity of experimentally evaluating these factors, theoretical modeling and large-scale observational data analysis across environmental gradients may be effective approaches to this topic.
- Generalizing biotic regulators of SNF. While recent work clearly demonstrates the importance of biotic factors such as N-fixer taxonomy, competition and herbivory as regulators of SNF, we currently lack a framework for generalizing and extrapolating the patterns of biotic regulation to large scales. Global forest census (gfbinitiative.org) and herbivory (Robinson et al. 2023) datasets will be useful tools for assessing the influence of competition, herbivory and plant taxonomy on biogeographic patterns of SNF.
- Understanding positive and negative effects of N-fixing trees on nonfixing neighbors. We currently lack consensus on when N-fixing trees promote versus inhibit growth of neighboring trees and the surrounding forest stand. Using a combination of forest census plots and manipulative experiments including and excluding N-fixing trees (e.g., Ortiz and Wolf 2024) in greenhouse experiments and forests that differ in dominant nonfixing tree species, soil N availability, climate, etc., will help us better determine what drives the impact of N-fixing trees on forest growth.
- Empirical SNF data from in situ global change experiments. To date, much of our evidence on how SNF will respond to global change is based on either small-scale growth chamber and greenhouse experiments or on observations of SNF across spatial gradients of environmental factors. As researchers increasingly overcome the challenges of conducting large-scale global change experiments in forests, it will be imperative to leverage these experiments to better understand forest SNF under future climate conditions.
- Improving mechanistic representation of SNF in ESMs. Creating mechanistic regulation of SNF in ESMs is a large task, but a critical one to accurately representing future global N and C dynamics. The current coupling of N inputs from fixation to plant productivity and N demand is valuable but risks ignoring scenarios where environmental regulation of N fixation is driven by factors that do not align well with plant productivity. Modeling SNF as a function of environmental variables such as light, temperature, soil N, etc. (as a few ESMs now do) will help improve the realistic representation of the process.
- Global standardized SNF measurements. A primary limitation to understanding and modeling SNF at global scales is a paucity of empirical data (particularly when compared to data on C cycling). Establishing global networks of coordinated standardized measurements of SNF in different ecosystems and environmental conditions would dramatically improve our understanding of this process—particularly in underrepresented regions such as tropical Africa and Asia.

Conclusions

Major advancements in our understanding of tree SNF have occurred over the past two decades, providing insight into phylogenetic, biogeographic and ecological patterns of this critical process. Traditional views of SNF as simply a ‘nitrostat’ regulator (SNF increases or decreases as a function of N limitation or saturation, respectively) of forest N availability are being replaced by the increasing recognition that this process is conducted by a wide variety of plant and bacterial taxa, that it is regulated by a complex suite of biotic and abiotic factors and that it can have important, but sometimes counterintuitive, impacts on the community dynamics and biogeochemical functioning of forest ecosystems. In the coming decades, both improved empirical data and theory development will be needed to quantify this spatially and temporally variable process and integrate it into our broader understanding of current and future forest function.

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Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Conflict of interest

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Data availability

All data and supporting analytical code are available at https://github.com/bentonneiltaylor/Tree-Physiology_Tree-SNF-Review.

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