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Article:

Menge, DNL, Batterman, SA, Liao, W et al. (2017) Nitrogen-fixing tree abundance in higher-latitude North America is not constrained by diversity. Ecology Letters, 20 (7). pp. 842-851. ISSN: 1461-023X

https://doi.org/10.1111/ele.12778

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Nitrogen-fixing tree abundance in higher-latitude North America is not constrained by diversity

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Running title: Diversity and N-fixing tree abundance

Keywords: Nitrogen, nitrogen fixation, symbiosis, legume, rhizobial, actinorhizal, latitude, America, Mexico, diversity

Submitted for consideration as a Letter in *Ecology Letters*

Number of words in abstract: 150

Number of words in main text: 5000

Number of references: 62

Number of figures: 5

Number of tables and text boxes: 1

Statement of authorship: DM developed the project, analyzed data, and wrote the first draft. SB helped develop the project and edited the manuscript. WL and BT analyzed data and edited the manuscript. JL and GAP provided data and edited the manuscript.

Data accessibility statement: Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad.

Abstract

The rarity of nitrogen (N)-fixing trees in frequently N-limited higher-latitude (here, >35°) forests is a central biogeochemical paradox. One hypothesis for their rarity is that evolutionary constraints limit N-fixing tree diversity, preventing N-fixing species from filling available niches in higher-latitude forests. Here we test this hypothesis using data from the U.S.A. and Mexico. N-fixing trees comprise only a slightly smaller fraction of taxa at higher vs. lower latitudes (8% vs. 11% of genera), despite 11-fold lower abundance (1.2% vs. 12.7% of basal area). Furthermore, N-fixing trees are abundant but belong to few species on tropical islands, suggesting low absolute diversity does not limit their abundance. Rhizobial taxa dominate N-fixing tree richness at lower latitudes, whereas actinorhizal species do at higher latitudes. Our results suggest that low diversity does not explain N-fixing trees' rarity in higher-latitude forests. Therefore, N limitation in higher-latitude forests likely results from ecological constraints on N fixation.

Introduction

Biological nitrogen (N) fixation brings more N into terrestrial ecosystems than any other natural input (Vitousek *et al.* 2013). Trees that form symbioses with N-fixing bacteria have the capacity to fuel symbiotic N fixation fluxes in excess of 100 kg N ha^{-1} yr^{-1} in tropical (Binkley & Giardina 1997), temperate (Binkley *et al.* 1994), and boreal (Ruess *et al.* 2009) forests. Such high fluxes far exceed the contribution from asymbiotic N-fixers (Reed *et al.* 2011) and abiotic N inputs in all but the most polluted ecosystems (Galloway *et al.* 2004), although realized fluxes of symbiotic N fixation are often much lower (e.g., Sullivan *et al.* 2014). Despite this huge capacity, many forest ecosystems remain N deficient (LeBauer & Treseder 2008), largely because of the absence or rarity of N-fixing trees (Vitousek & Howarth 1991). Hereafter, we refer to tree species capable of forming N-fixing symbioses as “N-fixing trees” for convenience, regardless of whether they are actively fixing N.

One striking example of the rarity of N-fixing trees appears across a latitudinal gradient in the Americas. For decades, scientists have noticed that N-fixing trees are comparatively rare in higher-latitude relative to lower-latitude American forests (Jenny 1950; Rundel 1989; Vitousek & Howarth 1991; Crews 1999). Recent studies with government-sponsored forest inventories, which are systematic, broad in geographic scale, and large in total sampling effort, have quantified this pattern in detail. N-fixing trees comprise around 10% of total trees in Amazonia (ter Steege *et al.* 2006) and around 10% of tree basal area in the U.S.A. and Mexico south of 35° N latitude, but around 1% of tree basal area in the coterminous U.S.A. north of 35° N (Menge *et al.* 2014).

While several hypotheses have been proposed to explain this transition in N-fixing tree abundance (Jenny 1950; Crews 1999; Houlton *et al.* 2008; Menge *et al.* 2014; Sheffer *et al.*

2015), our focus here is the possibility that low N-fixing tree diversity at higher latitudes might constrain N-fixing tree abundance (Crews 1999). N-fixing trees are undoubtedly less taxonomically rich at higher than lower latitudes, but the same is true for nearly all taxa (Hillebrand 2004). To test the hypothesis that taxonomic diversity limits N-fixing tree abundance at higher latitudes, it is critical to understand the *relative* diversity—the proportion of tree taxonomic richness—of N-fixing trees, and how their relative diversity compares to their relative abundance. The hypothesis that N-fixing tree diversity constrains N-fixing tree abundance at higher latitudes would be supported if N-fixing taxa comprised a much smaller fraction of total tree taxa at higher than lower latitudes. By contrast, a similar fraction of N-fixing taxa at higher and lower latitudes would suggest that they have diversified in and/or colonized higher latitudes as successfully as non-fixing trees, which would reject the hypothesis that their diversity constrains their abundance. However, there has yet to be a systematic assessment of how relative N-fixing tree diversity changes across latitude or how it relates to N-fixing tree relative abundance across latitude. Although our focus is on relative diversity, we also consider the role of absolute N-fixing tree diversity, which could factor in via sampling effects (Hector *et al.* 2002), by studying how lower-latitude islands compare to the continent. Diversity might be driven by different factors on islands vs. continents (MacArthur & Wilson 1967), so the comparison is not perfect, but the lower absolute richness on lower-latitude islands provides a natural test for the role of absolute richness.

When considering the taxonomic diversity of N-fixing trees, it is important to note that there are two major types of symbiotic N-fixing tree, rhizobial and actinorhizal. Rhizobial N-fixers are legumes (and *Parasponia*) that form symbioses with *Rhizobia*-type bacteria (Sprent 2009), whereas actinorhizal N-fixers are plants from eight other plant families that form symbioses with *Frankia*-type bacteria (Huss-Danell 1997). Although rhizobial trees are incredibly diverse globally (Sprent 2009; Werner *et al.* 2014), they are species-poor outside the tropics (Rundel 1989; Crews 1999), leading Crews (1999) to suggest that there are too few N-fixing legume tree species to fill the available niche space for symbiotic N-fixers at higher latitudes. Given that all species are less diverse at higher latitudes, however, their contribution to relative diversity is not yet as clear. Actinorhizal species contribute more than legumes to tree diversity (both absolute and relative) at higher latitudes (Benson and Dawson 2007; Menge *et al.* 2010; 2014), but are largely confined to early stages of succession (Benson and Silvester 1993).

Here, we use national forest inventories from Mexico and the U.S.A., including Alaska and tropical islands, to fill these gaps. Because we are using a newer and larger dataset than Menge *et al.* (2014), we first update the latitudinal pattern of N-fixing tree abundance and establish the lower-latitude continental vs. island pattern. We then ask two questions about patterns within the continent: (Q1) How does N-fixing tree diversity, as a proportion of total tree taxa, change across latitude? (Q2) How does the relationship between relative abundance and relative diversity of N-fixing trees change across latitude? We expect that the answers to these questions lie along a spectrum (Fig. 1). At one end of the spectrum, relative diversity of N-fixing trees might be much lower at higher than lower latitudes, but the relationship between abundance and diversity might be similar across latitudes. This end of the spectrum, depicted as a solid blue line compared to the solid red line in Fig. 1, would be consistent with the hypothesis that diversity is a major constraint on N-fixing tree abundance at higher latitudes. At the opposite end of the spectrum, relative diversity of N-fixing trees might be similar across latitudes, but N-fixing tree abundance might increase more slowly with N-fixing diversity at higher latitudes compared to lower latitudes. This other end of the spectrum, depicted as a dashed blue line compared to the solid red line in Fig. 1, would reject the hypothesis that diversity is a major constraint on N-fixing tree abundance at higher latitudes. Because these are two ends of a spectrum, we also ask a third question: (Q3) What fraction of the latitudinal abundance pattern can be explained by differential relative diversity versus differential abundance per relative diversity? Finally, we assess how tropical islands compare to the lower-latitude continent, which helps disentangle the role of absolute diversity. The key results we document below are that the relative diversity of N-fixing trees at higher latitudes is nearly as high as it is at lower latitudes, that relative diversity is unlikely to drive much of the latitudinal abundance pattern of N-fixing trees, and that low absolute diversity does not limit N-fixing tree abundance on the islands.

Methods

We investigated our questions in a variety of ways. Symbiotic N fixation is largely a genus-level trait (Sprent 2009; Werner *et al.* 2014), so we investigated taxonomic diversity at the genus level as well as the species level. Due to the major functional and phylogenetic differences between rhizobial and actinorhizal N-fixers (Menge *et al.* 2014; Werner *et al.* 2014), we investigated these questions for all N-fixers together, and also for rhizobial fixers and actinorhizal fixers separately. In some sites N-fixing trees comprise a distinctly different proportion of tree basal area than proportion of individual trees (Menge & Chazdon 2016), so we investigated both abundance metrics: relative basal area and relative individual density. For measurements where the total amount of area sampled might matter, we used the classic species-area relationship (Preston 1962) to scale our data to a similar area.

Forest inventory data

Forest inventory data come from the U.S. Forest Service's Forest Inventory and Analysis (FIA), version 5.1 (data available online at http://www.fia.fs.fed.us/) and the Mexican Comisión Nacional Forestal's Inventario Nacional Forestal y de Suelos (INFyS) 2004-2007. In both datasets, plots are systematically located across the land surface, at a density of one randomly-located plot per ~2,400 and ~2,500 ha forested land in the U.S. and Mexico, respectively. We excluded plots listed as plantations. Our dataset includes 331,447 plot records and 11,962,355 individual tree records (Table 1, Figs. 2a, S1a). Menge *et al.* (2014) used the same INFyS dataset, but an earlier version of the FIA dataset that did not include plots in Alaska or tropical islands. Plot record densities in individual 1° latitude x 1° longitude grid cells are displayed in Fig. 2a. Details of plot structure and sampling can be found in Menge *et al*. (2014). As in Menge *et al.* (2014), results here use only individual tree stems ≥ 7.5 cm diameter at breast height (dbh) to standardize the comparison across the FIA and INFyS datasets. When quantifying total sampling effort (e.g., in Table 1) we list all plot records (including multiple measurements from some plots), whereas for calculations that concern area we only count each unique plot once.

N-fixing species determination

We classified taxa as N-fixers, non-fixers, or unknown according to Huss-Danell (1997) for actinorhizals and Sprent (2009) for rhizobials. Because N fixation is essentially a genus-level trait (Sprent 2009; Werner *et al.* 2014) and there are many species that have not been examined, we classified all species with congeners listed in Sprent (2009) or Huss-Danell (1997) as capable of N fixation. This differs from the classification scheme in Menge *et al.* (2014), which also used information from the GRIN database, but our current method excludes only five species, representing 155 individual trees, that would be included from the GRIN criterion used in Menge *et al.* (2014). The only species we classified as an N-fixer that did not have congeners listed in Huss-Danell (1997) or Sprent (2009) was *Morella faya*, which was synonymous with *Myrica faya* in 1997 and is well known to be an actinorhizal N-fixer. We have not classified species as exotic vs. native; our analysis includes all species in the FIA and INFyS datasets.

Relative abundance, relative taxonomic richness, and absolute taxonomic richness

We calculated relative abundance as both the percentage of basal area and the percentage of individuals. To calculate basal area (BA) for each tree we assumed circular stems and used each tree's recorded dbh: $BA = \pi \left(\frac{dbh}{2}\right)^2$. For both metrics, we calculated relative abundance for each grid cell as the fraction of basal area or individual trees comprised of N-fixing (or rhizobial, or actinorhizal) taxa. Latitudinal means are the means of all grid cells in the continent with the same latitude. Island means are the means within each island or island group. Relative taxonomic richness, for either species or genera, was calculated as the fraction of total taxa comprised of N-fixing (or rhizobial, or actinorhizal) taxa in an island or degree latitude.

To compare the total numbers of taxa (absolute richness), we extrapolated to a standard area for each degree of latitude for continental plots. We also extrapolated to the same standard area for each island group. We used the classic power law relationship from Preston (1962), $S = cA^z$, where S is the number of taxa (species or genera), A is area sampled, and c (taxa per area to the z^{th} power) and z (unitless) are parameters defining the relationship between area and taxa. Area sampled, A, was calculated as the sum of standard subplot area in a given region, where the standard subplots are those used to sample adult trees of standard size in the INFyS and FIA datasets (see above). We used a common value of z, 0.25, fit c for each degree of latitude and taxonomic group, and extrapolated the number of taxa we would expect for the average area sampled per degree latitude in our data. We conducted these analyses for each taxonomic scale (species or genera) and N-fixing group (all taxa, all N-fixers, rhizobial N-fixers, and actinorhizal N-fixers). We did not make these corrections for relative taxonomic richness because it is a proportion, and thus independent of sampling area.

Statistical tests

To test whether N-fixing tree taxa are more or less abundant and diverse at lower latitudes vs. higher latitudes vs. islands, we conducted anovas and post-hoc Tukey HSD tests on latitude- and island-scale data. To test whether N-fixing tree taxa are disproportionately rare compared to their taxonomic richness at higher vs. lower latitude vs. islands, we compared the slopes of linear regressions forced through zero of relative abundance as functions of relative taxonomic richness. For both analyses, we used 35° as our primary latitudinal cutoff because 35° is the transition point for N-fixing tree abundance in North America (Menge *et al.* 2014). To assess sensitivity to this cutoff, we conducted analyses using every two latitudinal degrees from 30° to 40° as the cutoff.

Results

We conducted our statistics at the latitude scale ($n = 55$), which vastly underestimates the true power of our data (331,447 plot records, 11,962,355 tree records; Table 1), yet still gives statistically significant results ($P < 0.05$) for all the trends we report in the text. However, because statistical significance does not necessarily indicate biological importance, we focus on effect sizes.

N-fixing taxa

Overall, our dataset included 3,348 species and 950 genera (Table 1). Of these, we classified 378 species (11%) and 68 genera (7%) as N-fixing taxa. Table S1 lists the species we classified as N-fixers.

N-fixing trees are an order of magnitude less abundant at higher latitudes

Our analyses confirm a threshold transition of N-fixing tree relative abundance at 35° latitude in North America. N-fixing trees are an order of magnitude more abundant (10.6 fold for basal area, 9.4 fold for individual trees) at lower (12.7% of basal area) than at higher (1.2% of basal area) latitudes (Figs. 2b, S1b, Table S2). The proportion of trees and the proportion of basal area show similar trends throughout our analyses, so we present basal area data in the main text and individual tree data in the Supplementary Material. The tropical islands in the inventory have average relative abundances (11.7% of basal area) that are similar to the lower-latitude continent (Figs. 2b, S1b, Table S2). The higher latitudes of Southeastern Alaska, from 54°-61°N, continue the trend of low relative abundance observed from 35°-49° in the coterminous U.S (Figs. 2b, S1b), although N-fixer abundance is even lower in Alaska (0.1% of basal area) than from 35°-49° (1.7%).

Rhizobial N-fixers (Figs. 2c, S1c) show similar trends to all N-fixers, although the latitudinal transition is even starker than it is for all N-fixers. Actinorhizal N-fixers are rare at all latitudes, and do not show a distinct latitudinal relative abundance trend (Figs. 2d, S1d).

N-fixing trees are less taxonomically rich at higher latitudes, as are all trees

There are nine times more N-fixing tree genera (30.6 vs. 3.4; Fig. 3a) and twenty times more N-fixing tree species (93.1 vs. 4.8; Fig. S2a) at lower latitudes than there are at higher latitudes (Table S3). This latitudinal disparity is sharper for Rhizobial taxa (26 and 67 fold; Figs. 3b, S2b). By contrast, actinorhizal species are only 1.6 times more genus-rich and 2 times more species-rich at higher latitudes than at lower latitudes (Fig. 3c, S2c). These patterns hold whether or not we correct for different sampling areas (Fig. S2e-l), and for a range of cutoffs used to define higher vs. lower latitudes (Table S3). Like N-fixing trees, all trees are also more taxon-rich (7 and 6 fold for genera and species) at lower latitudes (Fig. 3d, S2d), so we focused our subsequent analyses on the relative taxonomic richness of N-fixing trees (percent of total genera or species comprised by N-fixing trees). Tropical islands are 84% and 39% as genus- and species rich as the lower-latitude continent when we standardize to the same area (Fig. 3a), but 38% and 17% as genus- and species-rich without standardizing (Fig. S2e,i).

Relative taxonomic richness of N-fixing trees varies across latitude to different degrees, depending on N-fixer type and taxonomic scale

Although N-fixing trees are less taxonomically rich at higher latitudes, their lower diversity scales almost proportionally with total tree taxonomic richness. As a proportion of tree genera at a given latitude, N-fixing trees are only 1.4 fold more diverse at lower latitudes (11%) than at higher latitudes (7.7%; Fig. 4a, Table S4), compared to the 10.6 fold greater relative abundance. Relative species richness differs slightly more across latitude (2.4 fold; 11.1% vs. 4.6%; Fig. S3a, Table S4) than relative genus richness. Relative rhizobial richness of genera and species shows a starker latitudinal decline (5 fold for genera, 16 fold for species; Fig. 4b, S3b, Table S4), whereas relative actinorhizal richness is actually higher at higher latitudes (3 and 4 fold for genera and species), driven largely by Alaska, where the lone N-fixing genus, *Alnus*, is one of only 11 total tree species in the dataset (Fig. 4c, S3c, Tables 1, S4). Relative diversity on islands is not significantly different than the lower-latitude continents for all N-fixer types (Fig. 4, S3, Table S4).

N-fixing tree rarity, not low N-fixing tree diversity, explains most of the abundance trend of N-fixing trees

All N-fixing trees have a similar range of relative genus richness at higher and lower latitudes and the tropical islands (Fig. 5a, S4a-S8a). However, the relationship between relative richness and abundance differs substantially across latitudes. At lower latitudes, N-fixing tree abundance lies near the 1:1 line with taxonomic richness (slope of 1.1), whereas at higher latitudes N-fixing trees are rare even when they comprise a large fraction of the taxon pool (slope of 0.12; Fig. 5a, Table S5). The ratio of slopes for higher vs. lower latitudes is 0.11 (Table S5), meaning that only about 11% of the abundance pattern across latitude can be explained by changes in taxonomic richness. This slope ratio is similar (0.08-0.15) for different metrics of abundance, taxonomic richness, and latitude cutoffs (Figs. S4-S8a, Table S5). On the tropical islands, the slope (1.5) is even higher than the lower-latitude continent (Figs. 5a, S4-S8a, Table S5).

The pattern is somewhat different for rhizobial (Fig. 5b) and actinorhizal (Fig. 5c) trees. Rhizobial trees do not have the same range of relative taxonomic richness at higher latitudes as do all N-fixing trees, so the slope ratio is more dependent on which metrics of relative abundance and richness we use. For basal area and genera, the slope ratio is 0.25 (Fig. 5b), whereas for other combinations it ranges from 0.09-1.00 (Table S5, Fig. S4b-S8b). As with all fixers, rhizobial trees had higher slopes on tropical islands than at lower latitudes on the continent.

Actinorhizal trees diverge from the pattern for all N-fixing trees in a different way. Actinorhizal trees are never abundant at the latitude scale, so all slopes are well below the 1:1 line. Furthermore, actinorhizals occupy a narrow range of relative taxonomic richness at *lower* latitudes, in contrast to rhizobials, so the lower latitude slopes vary more. Overall, the actinorhizal slope ratios range from 0.17-0.81 (Table S5, Figs. 5c, S4c-S8c).

Discussion

When we consider all N-fixing trees as a single group, our results do not support the hypothesis that evolutionary constraints explain the low N-fixing tree abundance at higher latitudes. Relative taxonomic richness of N-fixing trees does not change much across latitude in North America, particularly at the genus level, whereas relative abundance of N-fixers declines dramatically above 35°N. The finding is somewhat different, however, if we focus on rhizobial and actinorhizal trees separately. Although N-fixing trees (rhizobial and actinorhizal combined) comprise a similar proportion of total tree taxa at higher vs. lower latitudes, rhizobial trees comprise a much smaller proportion of taxa at higher latitudes, where actinorhizal trees are the majority of N-fixing tree taxa. The slopes in Figs. 5b and S4b indicate that rhizobial genera are disproportionately rare at higher latitudes even given this low diversity, but the species level results (Figs. S5b, S6b) suggest that low diversity is the dominant driver. By contrast, actinorhizal genera are similarly rare at lower vs. higher latitude regardless of their diversity (Figs. 5c, S4-S8c).

Based on the results presented here, therefore, the argument for diversity limitation only holds if rhizobial diversity, not actinorhizal diversity, is the limiting factor. This argument would require two components. First, actinorhizal N-fixing tree taxa would need to be inherently limited in their capacity to fill a wide range of niche space over evolutionary time. Second, rhizobial N-fixing tree taxa would need to be inherently limited in their capacity to reach higher latitudes over evolutionary time. Neither component is particularly plausible. Actinorhizal trees come from a large clade of angiosperms (Soltis *et al.* 1995; Werner *et al.* 2014) that is well represented in all successional stages of North American forests (Menge *et al.* 2010), so the idea that N fixation has not appeared with the other traits needed to succeed in a broader range of habitats is unlikely. It is possible that actinorhizal trees are evolutionarily confined to an obligate N fixation strategy, which might prevent them from filling a wide array of niche space (Crews 2016). However, it is at least as plausible that they have specialized in an obligate N fixation strategy for ecological reasons (Menge et al. 2009, Sheffer et al. 2015), which would indicate that the niche space for N-fixing trees is simply narrow. On the rhizobial side, a model of neutral trait evolution estimated that thousands of species of higher-latitude woody N-fixing legumes would have evolved if N fixation were as adaptive at higher latitudes as it is at lower latitudes (Menge & Crews 2016). That study also argued that post-glacial dispersal limitation (Svenning & Skov 2007) is unlikely to preferentially affect legumes, based on dispersal mechanisms and the observation that legumes are equally rare at high altitudes in Mexico as they are at higher latitudes (Menge *et al.* 2014). Therefore, the idea that diversity limits N-fixing tree abundance at higher latitudes lacks support. Rather, the most likely scenario is that the available niche space for N-fixing trees at higher latitude is narrow and filled by actinorhizal species.

What is the niche for N-fixing trees at higher latitudes? It has long been observed that N-fixing trees outside the tropics are pioneer species (e.g., Wardle 1980; Gutschick 1981; Boring *et al.* 1988; Vitousek & Howarth 1991; Chapin *et al.* 1994), as analyses with the U.S. FIA data confirm (Menge *et al.* 2010). However, N-fixing trees are still fairly rare in young forests in the

U.S.A. (~0.75% of basal area in the east and ~5% in the west for forests 0-50 years old; Menge *et al.* 2010), so their niche is a small subset of early successional forests. The combined roles of light and N likely play major roles in defining this niche, and other factors such as herbivory, pathogens, or the availability of other nutrients might also play roles (Vitousek & Howarth 1991).

The observation that N fixation is energetically expensive (Gutschick 1981) has been used to argue that light availability might help constrain N-fixing trees to early-successional niches (Vitousek & Howarth 1991; Vitousek & Field 1999; Rastetter *et al.* 2001). N-fixing trees in the U.S. FIA plots are shade intolerant (Menge *et al.* 2010), supporting this idea, but a number of lines of evidence suggest that light is not the only factor. First, as mentioned above, N-fixing trees are rare even in young forests (Menge *et al.* 2010), where most canopy trees have regenerated under high-light conditions. Second, N-fixing trees in the canopy of U.S. FIA plots have lower growth rates and higher mortality rates than non-fixing trees in the canopy, just as they do in the understory (Liao & Menge 2016). Third, even when exposed to plenty of light, trees do not always fix N. In a lowland tropical forest in Panama, fixation rates were 15-fold lower in mature forests than in young successional forests, even though N-fixing trees in both forest types had similar access to the canopy (Batterman *et al* 2013). Together, these observations suggest that there is another major constraint in addition to light.

Soil N availability is another obvious factor that could explain niche constraints on N-fixing trees at higher latitudes. At the beginning of secondary succession, N availability is often high because N mineralization continues despite a drop in soil N uptake (Vitousek & Reiners 1975; Houlton *et al.* 2003). This temporary flush of soil N could disfavor N-fixing trees during the initial stages of succession, so even if N availability declines later in succession, N-fixing trees might be sufficiently shaded that they cannot recover (Vitousek & Howarth 1991). Overall, the niche for N-fixing trees is likely to be the subset of young forests that have both high light penetration and extremely low soil N availability.

Most of the above light- and N-based mechanisms would influence the cost-effectiveness of N fixation itself, but would not necessarily influence the plant as a whole. A shady understory or high soil N availability might make N fixation cost-ineffective, but that would not matter if N-fixing plants can use soil N instead of fixed N without incurring a cost. Therefore, a key but often unspecified component of this niche argument is that N-fixing trees must either continue to rely on N fixation when it is cost-ineffective, or they must incur some cost of being able to fix N (Menge *et al.* 2009). There is some evidence that N-fixing trees at higher latitudes continue to fix N at high rates even under high soil N conditions (Mead & Preston 1992; Binkley *et al.* 1994; Menge & Hedin 2009), suggesting that they are either ecologically obligate (they fix at similar rates under natural conditions, even if they do not need to for survival) or that they incompletely down-regulate N fixation (Menge *et al.* 2015). By contrast, many N-fixing trees at lower latitudes seem to be facultative (Barron *et al.* 2011; Batterman *et al.* 2013; Sullivan *et al.* 2014), down-regulating N fixation under high N conditions, which would help explain their greater prevalence (Menge *et al.* 2014; Sheffer *et al.* 2015). A possible cost of being able to fix N is that exposure to symbiotic bacteria leads to lower N use efficiency, even for plants that are not fixing (Menge *et al.* 2015; Wolf *et al.* 2016).

Our focus so far has been on relative diversity, but we now consider absolute diversity. In tropical forests where the species pools are larger, N-fixing trees differ widely in their successional habits (Batterman *et al.* 2013), N fixation rates (Wurzburger & Hedin 2016), foliar N contents (Bhaskar *et al.* 2016), and other traits (Rundel 1989; McKey 1994). With a smaller overall species pool at higher latitudes, could a sampling effect (e.g., Hector *et al.* 2002), whereby random chance has selected a series of poor-performing N-fixing tree species, explain the low abundance of N-fixing trees? We find an absolute diversity constraint unlikely for two reasons: (1) Our tropical islands results, and (2) The potential species pool. (1) Tropical islands have low absolute diversity of N-fixing trees like higher latitudes, but a tropical environment like lower latitudes, so they provide a natural way to disentangle the effect of absolute diversity from the effect of different environments. The fact that relative N-fixing tree diversity and abundance are similar in the islands and the lower-latitude continent suggests that low absolute diversity does not constrain N-fixing tree abundance. (2) A sampling effect concerns the potential species pool, not the existing species pool. The estimate that thousands of rhizobial N-fixing tree taxa have had the chance to colonize higher-latitude forests (Menge & Crews 2016) suggests that a wide species pool has been available, but has been unsuccessful. Given this large potential species pool, it is unlikely that the species that have colonized higher latitudes successfully are poor performers by random chance.

We have focused on higher- vs. lower-latitudes, but the trends within lower latitudes are also interesting. Relative abundance is proportional to relative diversity for all N-fixing trees and for rhizobial trees at low latitudes, but with wide variation around the trend. We have not directly addressed drivers of this variation, but aridity is an intriguing possibility. Our lower latitude sites range from arid to exceptionally wet (Liao *et al.* 2017), and recent work has established that N-fixing and particularly rhizobial trees are more abundant in drier sites, both in these datasets (Liao *et al.* 2017) and elsewhere in the tropics (Pellegrini *et al*. 2016).

Overall, we find the argument that narrow niche space explains low N-fixing tree abundance in higher-latitude forests to be much more persuasive than the argument that diversity constrains N-fixing tree abundance. Additional ways to test these conclusions include assessing patterns on other continents or in the paleo-ecological record. For example, if N-fixing trees are rare at higher latitudes in other continents—and if N-fixing trees were rare at higher latitudes during previous interglacials and other periods with similar climate—despite comprising a similar fraction of tree diversity at higher and lower latitudes, a niche-based explanation would seem even more likely.

The approach we develop here—comparing slopes of relative abundance of a functional group against its relative diversity across categories—could be used in a variety of contexts to assess whether diversity of a group limits its abundance. For example, lianas (Schnitzer 2005), arbuscular (as opposed to ecto or ericoid) mycorrhizal associations (Allen *et al*. 1995) and C_4 (as opposed to C_3) photosynthetic pathways (Still *et al*. 2003) are common at lower latitudes but rare at higher latitudes.

The rarity of N-fixing trees in higher-latitude forests is a key component of a central biogeochemical paradox, the persistence of N limitation (Vitousek & Howarth 1991). Our results here support the idea that niche-based mechanisms are the culprit, and should therefore help focus future efforts to understand both the rarity of N-fixing trees and, ultimately, the persistence of N limitation. Understanding of N limitation in general (Hungate *et al.* 2003; Sokolov *et al.* 2008; Gerber *et al.* 2010; Zaehle *et al.* 2010; Thomas *et al.* 2013; Wårlind *et al.* 2014), and of the role of symbiotic N-fixers in particular (Stocker *et al.* 2016), have been highlighted as key uncertainties in global carbon-cycle and climate projections. Our results suggest that future efforts to study N-fixing trees and N fixation, and thus to better understand global carbon storage and climate, should focus on niche-based ecological mechanisms.

Acknowledgements

Mexico's Comisión Nacional Forestal provided the Mexican forest inventory data. This material is based upon work supported by the National Science Foundation under grant no. DEB-1457650. SAB was supported by a U.K. Natural Environment Research Council Independent Research Fellowship (NE/M019497/1).

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Tables

Table 1: Plot records, individual tree records, and taxa by region.

Region	# plot records	# tree records*	# genera*	# species*
Coterminous U.S.	312,332	10,713,005 (79,635)	100 (11)	370 (21)
Mexico	15,305	1,097,517 (147,378)	771 (61)	2,585 (337)
Southeastern Alaska	2,865	111,858 (526)	11 (1)	17 (1)
Puerto Rico	405	13,667 (2,093)	208 (19)	341 (29)
Hawaiian islands	205	14,211 (1,769)	55 (9)	77 (9)
Palau	110	4,761 (29)	101 (5)	136 (5)
Guam	86	2,352 (291)	50 (3)	59 (4)
U.S. Virgin Islands	65	2,558 (722)	90 (9)	121 (14)
American Samoa	41	1,234 (25)	60 (2)	79 (3)
Total	**331,447**	**11,962,355 (232,694)**	**950 (68)**	**3,348 (378)**

*Numbers out of parentheses include all trees; those in parentheses are N-fixing trees only.

Figure captions

Fig. 1. Conceptual model of competing hypotheses. The dotted black line indicates the 1:1 line. Values on this line indicate that relative nitrogen (N)-fixing tree abundance is proportional to relative N-fixing tree taxonomic richness, whereas values off the line indicate that N-fixing trees are disproportionately abundant (above the 1:1 line) or disproportionately rare (below the 1:1 line) compared to their richness. The red line indicates a hypothesized trend in lower-latitude forests, and the blue lines indicate competing hypotheses for higher-latitude forests. Circles are means of the hypothesized trends. Both competing hypotheses capture the established trend that lower latitudes have ten-fold higher mean abundance of N-fixing trees than higher latitudes (vertical values of red compared to blue circles). The hypotheses differ in the relationship between relative richness and relative abundance. The solid blue line (hypothesis 1) indicates that the rarity of N-fixing trees in higher-latitude forests results from reduced relative diversity (lower mean richness) but not disproportionate rarity (same slope as red line). At the opposite end of the spectrum, the dashed blue line (hypothesis 2) indicates that N-fixer rarity results from reduced abundance per diversity (lower slope) but not reduced relative diversity (same mean richness for blue and red).

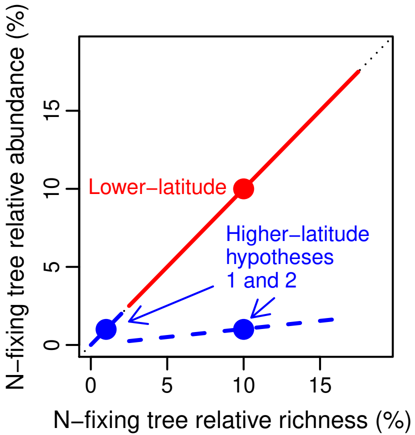
Fig. 2. Nitrogen (N)-fixing tree relative abundance across latitude. Data are from systematic national forest inventories in the United States and Mexico. (a) The total number of plot records in each 1° latitude by 1° longitude grid cell is shown with color on a log scale. (b) Relative abundance (% of total tree basal area) of all N-fixing trees. Open circles are means of all 1° latitude by longitude grid cells on the continent. Other symbols are means within islands or island chains, none of which spans more than 1° latitude. Means are shown for islands (dashed

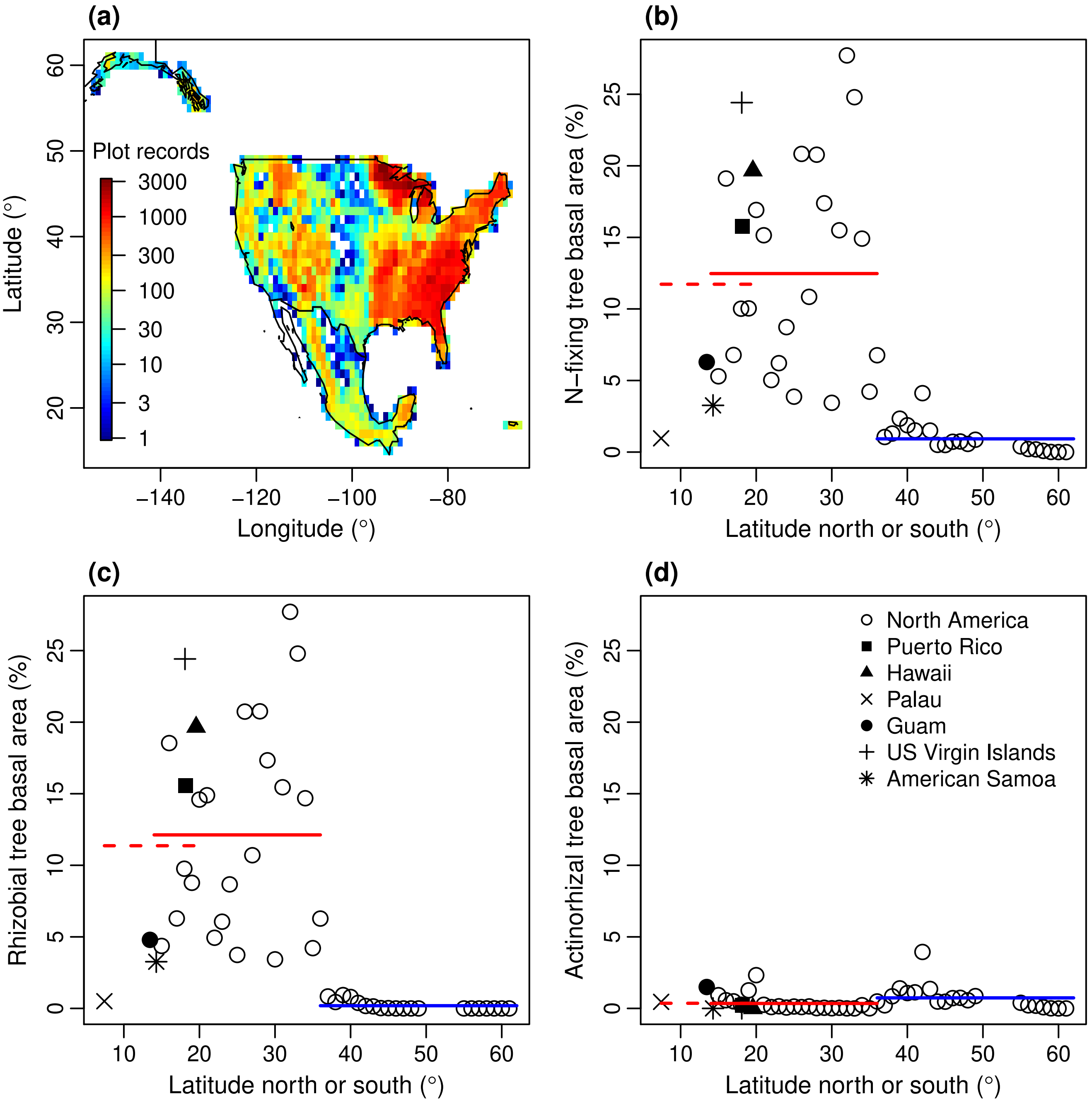
red) and for lower- (solid red) and higher- (blue) latitude continental data, using 35° as the cutoff. Data are also displayed for (c) rhizobial N-fixers and (d) actinorhizal N-fixers.

Fig. 3. Tree genus richness in a standardized area across latitude. (a) Genus richness of all N-fixing trees is shown as the number of genera in each 1° latitude. Area sampled differs substantially across latitude, as shown in Fig. S1a, so these data are standardized to the mean area sampled for a given latitude. Uncorrected genus richness data, which are more relevant for comparing islands to the continent, are shown in Fig. S2. Symbols and fits follow Fig. 2. Genus richness of (b) rhizobial and (c) actinorhizal N-fixers as well as (d) all trees are also shown.

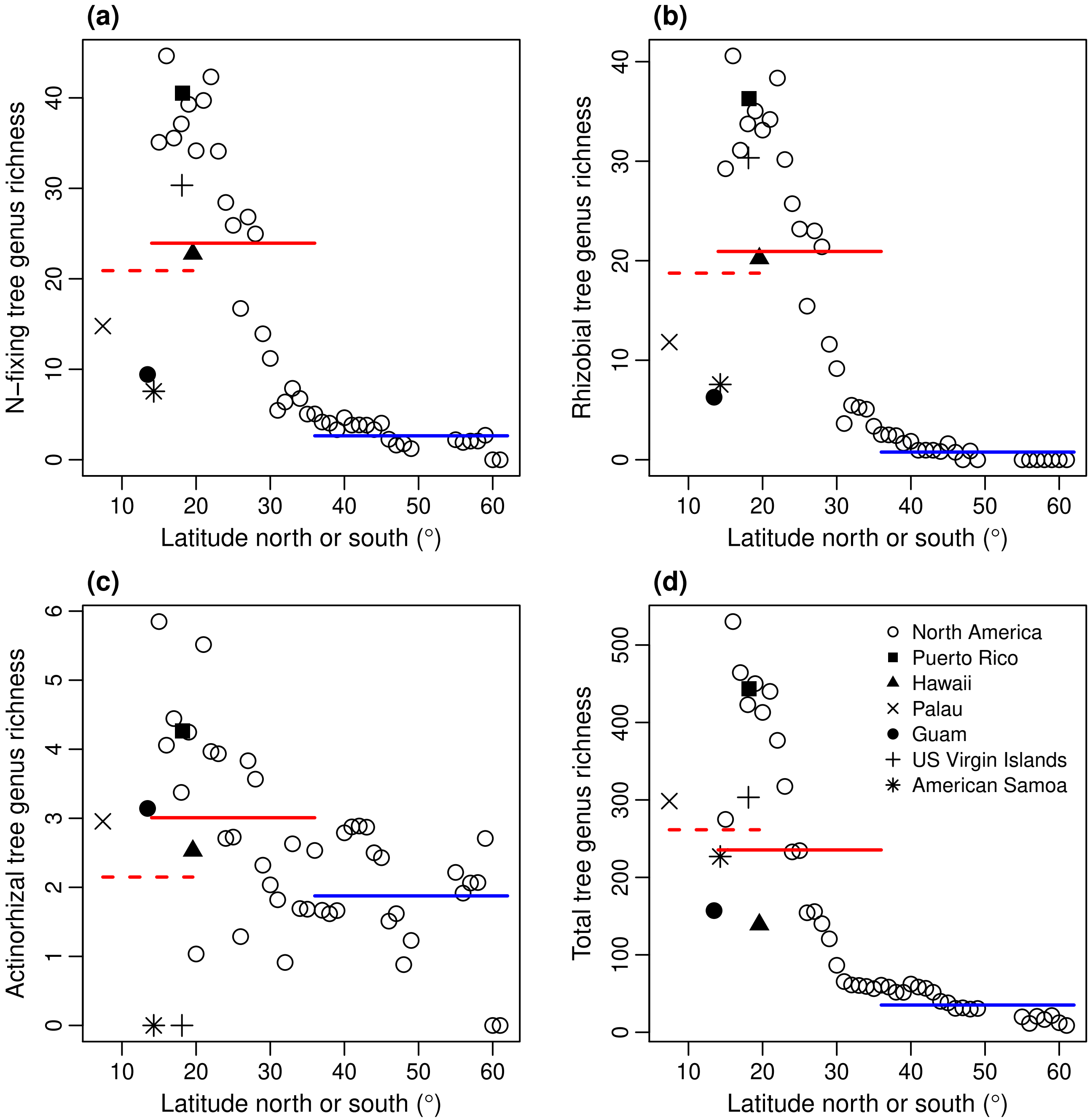
Fig. 4. Relative genus richness of N-fixing trees across latitude. The percent of all tree genera that are (a) N-fixing, (b) rhizobial, and (c) actinorhizal are shown as a function of latitude. Symbols and fits follow Fig. 2.

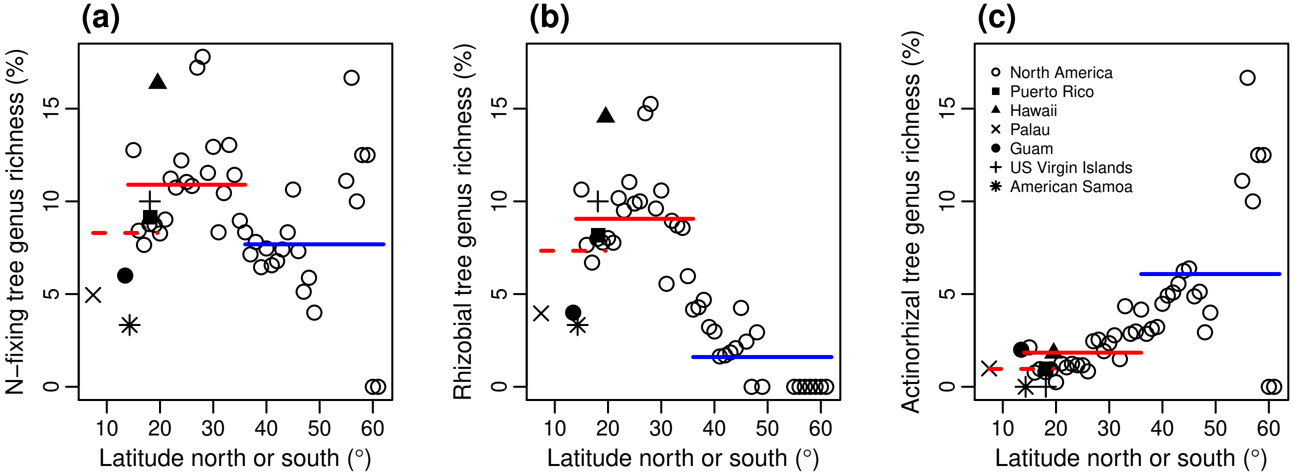
Fig. 5. N-fixing tree relative basal area as a function of relative genus richness of N-fixing trees. Lower-latitude (red open circles, red solid line; < 35°) and higher-latitude (blue triangles, blue line; > 35°) continental data and fits are shown along with tropical islands (filled symbols and red dashed line). R^2 values shown in each panel are adjusted R^2s for the overall model (all lines in the panel). The 1:1 line is shown as a dotted black line. Data and fits are shown for (a) all N-fixers, (b) rhizobial N-fixers, and (c) actinorhizal N-fixers. Figs. S4-S6 show alternate versions with the proportion of individual trees instead of basal area, and species richness instead of genus richness. Figs. S7-S8 show alternate cutoffs for higher vs. lower latitude (35° in this figure).

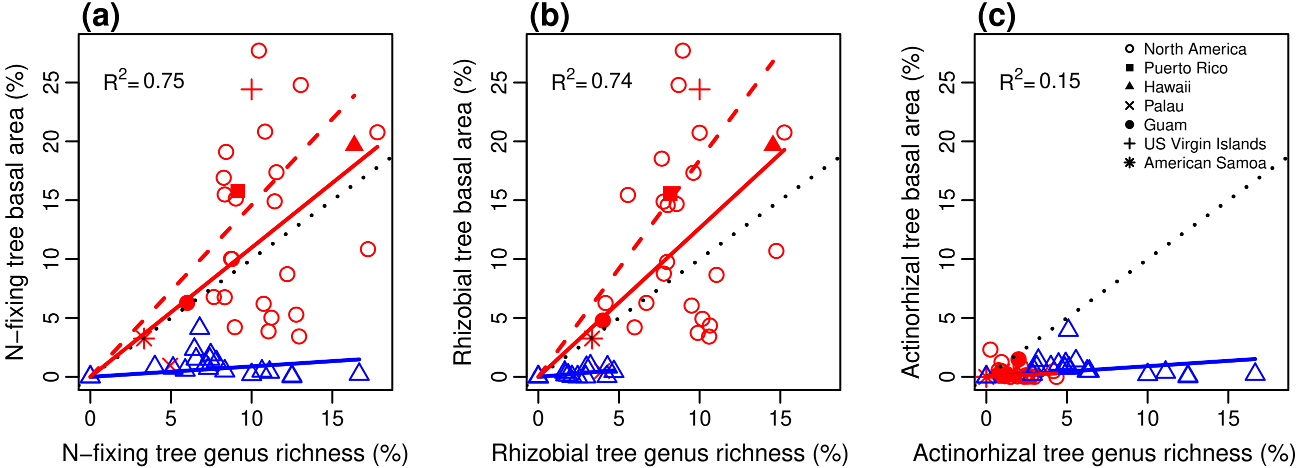

N–fixing tree relative abundance (%)
0
5
10
15
N–fixing tree relative richness (%)
0
5
10
15
Lower–latitude
Higher–latitude
hypotheses
1 and 2



(a)
Plot records
3000
1000
300
100
30
10
3
1
Latitude (°)
Longitude (°)
(b)
N−fixing tree basal area (%)
Latitude north or south (°)
(c)
Rhizobial tree basal area (%)
Latitude north or south (°)
(d)
Actinorhizal tree basal area (%)
Latitude north or south (°)
○ North America
■ Puerto Rico
▲ Hawaii
× Palau
● Guam
+ US Virgin Islands
✳ American Samoa


(a)
N−fixing tree genus richness
0
10
20
30
40
10
20
30
40
50
60
Latitude north or south (°)
(b)
Rhizobial tree genus richness
0
10
20
30
40
10
20
30
40
50
60
Latitude north or south (°)
(c)
Actinorhizal tree genus richness
0
1
2
3
4
5
6
10
20
30
40
50
60
Latitude north or south (°)
(d)
Total tree genus richness
0
100
200
300
400
500
10
20
30
40
50
60
Latitude north or south (°)
○ North America
■ Puerto Rico
▲ Hawaii
× Palau
● Guam
+ US Virgin Islands
✳ American Samoa


(a)
(b)
(c)
N–fixing tree genus richness (%)
Rhizobial tree genus richness (%)
Actinorhizal tree genus richness (%)
0
5
10
15
10
20
30
40
50
60
Latitude north or south (°)
North America
Puerto Rico
Hawaii
Palau
Guam
US Virgin Islands
American Samoa


(a)
R^2= 0.75
N–fixing tree basal area (%)
N–fixing tree genus richness (%)
(b)
R^2= 0.74
Rhizobial tree basal area (%)
Rhizobial tree genus richness (%)
(c)
R^2= 0.15
Actinorhizal tree basal area (%)
Actinorhizal tree genus richness (%)
0
5
10
15
20
25
○ North America
■ Puerto Rico
▲ Hawaii
× Palau
● Guam
+ US Virgin Islands
✱ American Samoa

Supplementary Information for

Nitrogen-fixing tree abundance in higher-latitude North America is not constrained by diversity

Duncan N. L. Menge, Sarah A. Batterman, Wenying Liao, Benton N. Taylor, Jeremy W. Lichstein, and Gregorio Ángeles-Pérez

Table S1. Nitrogen (N)-fixing species in our dataset.

Table S2. Higher and lower latitude relative abundance means for all N-fixers.

Table S3. Taxonomic richness for a standardized area in each degree of latitude or island group.

Table S4. Relative taxonomic richness for each degree of latitude or island group.

Table S5. Fits for relative abundance against relative richness.

Figure S1. Nitrogen (N)-fixing tree relative abundance across latitude for proportion of individual trees.

Figure S2. N-fixing tree taxonomic richness across latitude.

Figure S3. N-fixing tree relative taxonomic richness across latitude.

Figure S4. N-fixing tree relative individual abundance as a function of relative genus richness.

Figure S5. N-fixing tree relative basal area as a function of relative species richness.

Figure S6. N-fixing tree relative individual abundance as a function of relative species richness.

Figure S7. N-fixing tree relative basal area as a function of relative genus richness for a 34° latitude cutoff.

Figure S8. N-fixing tree relative basal area as a function of relative genus richness for a 36° latitude cutoff.

Tables

Table S1. Nitrogen (N)-fixing species in our dataset.

Species	N-fixing type
Abarema cochleata	Rhizobial
Abarema jupunba	Rhizobial
Acacia acatlensis	Rhizobial
Acacia amentacea	Rhizobial
Acacia anegadensis	Rhizobial
Acacia angustissima	Rhizobial
Acacia berlandieri	Rhizobial
Acacia biflora	Rhizobial
Acacia bilimekii	Rhizobial
Acacia brandegeana	Rhizobial
Acacia californica	Rhizobial
Acacia centralis	Rhizobial
Acacia cochliacantha	Rhizobial
Acacia collinsii	Rhizobial
Acacia confusa	Rhizobial
Acacia constricta	Rhizobial
Acacia cornigera	Rhizobial
Acacia coulteri	Rhizobial
Acacia cyanophylla	Rhizobial
Acacia cymbispina	Rhizobial
Acacia dolichostachya	Rhizobial
Acacia dolicocephala	Rhizobial
Acacia farnesiana	Rhizobial
Acacia fasciculata	Rhizobial
Acacia galpini	Rhizobial
Acacia gaumeri	Rhizobial
Acacia glandulifera	Rhizobial
Acacia globulifera	Rhizobial
Acacia glomerosa	Rhizobial
Acacia greggii	Rhizobial
Acacia hindsii	Rhizobial
Acacia iguana	Rhizobial
Acacia koa	Rhizobial
Acacia macilenta	Rhizobial
Acacia macracantha	Rhizobial
Acacia melanoceras	Rhizobial
Acacia micrantha	Rhizobial
Acacia millefolia	Rhizobial
Acacia milleriana	Rhizobial
Acacia muricata	Rhizobial
Acacia neovernicosa	Rhizobial
Acacia occidentalis	Rhizobial

Acacia olgana	Rhizobial
Acacia palmeri	Rhizobial
Acacia paniculata	Rhizobial
Acacia penicillata	Rhizobial
Acacia peninsularis	Rhizobial
Acacia pennatula	Rhizobial
Acacia polyphylla	Rhizobial
Acacia pringlei	Rhizobial
Acacia rigidula	Rhizobial
Acacia riparia	Rhizobial
Acacia schaffneri	Rhizobial
Acacia sphaerocephala	Rhizobial
Acacia spp.	Rhizobial
Acacia tenuifolia	Rhizobial
Acacia vernicosa	Rhizobial
Acacia willardiana	Rhizobial
Acacia wrightii	Rhizobial
Aeschynomene ciliata	Rhizobial
Aeschynomene hintonii	Rhizobial
Albizia carbonaria	Rhizobial
Albizia caribaea	Rhizobial
Albizia julibrissin	Rhizobial
Albizia lebbeck	Rhizobial
Albizia leucocalyx	Rhizobial
Albizia longepedata	Rhizobial
Albizia niopoides	Rhizobial
Albizia occidentalis	Rhizobial
Albizia procera	Rhizobial
Albizia purpusii	Rhizobial
Albizia sinaloensis	Rhizobial
Albizia tomentosa	Rhizobial
Alnus acuminata	Actinorhizal
Alnus arguta	Actinorhizal
Alnus firmifolia	Actinorhizal
Alnus glabrata	Actinorhizal
Alnus glutinosa	Actinorhizal
Alnus jorullensis	Actinorhizal
Alnus oblongifolia	Actinorhizal
Alnus rhombifolia	Actinorhizal
Alnus rubra	Actinorhizal
Alnus spp.	Actinorhizal
Andira galeottiana	Rhizobial
Andira inermis	Rhizobial
Ateleia pterocarpa	Rhizobial
Brongniartia alamosana	Rhizobial
Calliandra belizensis	Rhizobial

Calliandra eriophylla	Rhizobial
Calliandra formosa	Rhizobial
Calliandra houstoniana	Rhizobial
Calliandra laevis	Rhizobial
Calliandra tonduzii	Rhizobial
Canavalia hirsuta	Rhizobial
Casuarina cunninghamiana	Actinorhizal
Casuarina equisetifolia	Actinorhizal
Casuarina lepidophloia	Actinorhizal
Casuarina spp.	Actinorhizal
Ceanothus caeruleus	Actinorhizal
Ceanothus greggii	Actinorhizal
Centrosema plumieri	Rhizobial
Centrosema schottii	Rhizobial
Centrosema virginianum	Rhizobial
Cercocarpus betuloides	Actinorhizal
Cercocarpus breviflorus	Actinorhizal
Cercocarpus fothergilloides	Actinorhizal
Cercocarpus ledifolius	Actinorhizal
Cercocarpus macrophyllus	Actinorhizal
Cercocarpus mojadensis	Actinorhizal
Cercocarpus montanus	Actinorhizal
Chloroleucon mangense	Rhizobial
Cojoba arborea	Rhizobial
Cojoba haematoloba	Rhizobial
Colutea arborescens	Rhizobial
Coursetia glandulosa	Rhizobial
Cowania mexicana	Actinorhizal
Cracca sericea	Rhizobial
Crotalaria cajanifolia	Rhizobial
Crotalaria longirostrata	Rhizobial
Crotalaria pumila	Rhizobial
Crotalaria rotundifolia	Rhizobial
Crotalaria vitellina	Rhizobial
Dalbergia brownei	Rhizobial
Dalbergia congestiflora	Rhizobial
Dalbergia funera	Rhizobial
Dalbergia glabra	Rhizobial
Dalbergia granadillo	Rhizobial
Dalbergia palo-escrito	Rhizobial
Dalbergia retusa	Rhizobial
Dalbergia sissoo	Rhizobial
Dalea capitata	Rhizobial
Desmanthus velutinus	Rhizobial
Desmanthus virgatus	Rhizobial
Desmodium cinereum	Rhizobial

Desmodium densiflorum	Rhizobial
Desmodium hirsutum	Rhizobial
Desmodium scorpiurus	Rhizobial
Diphysa americana	Rhizobial
Diphysa carthagenensis	Rhizobial
Diphysa floribunda	Rhizobial
Diphysa macrophylla	Rhizobial
Diphysa minutifolia	Rhizobial
Diphysa occidentalis	Rhizobial
Diphysa puberulenta	Rhizobial
Diphysa robinioides	Rhizobial
Diphysa suberosa	Rhizobial
Dussia cuscatlanica	Rhizobial
Ebenopsis confinis	Rhizobial
Ebenopsis ebano	Rhizobial
Elaeagnus angustifolia	Actinorhizal
Entada phaseoloides	Rhizobial
Entada polystachya	Rhizobial
Enterolobium cyclocarpum	Rhizobial
Eriosema grandiflorum	Rhizobial
Erythrina americana	Rhizobial
Erythrina berteriana	Rhizobial
Erythrina breviflora	Rhizobial
Erythrina caribaea	Rhizobial
Erythrina coralloides	Rhizobial
Erythrina flabelliformis	Rhizobial
Erythrina folkersii	Rhizobial
Erythrina fusca	Rhizobial
Erythrina glauca	Rhizobial
Erythrina goldmanii	Rhizobial
Erythrina herbacea	Rhizobial
Erythrina lanata	Rhizobial
Erythrina leptorhiza	Rhizobial
Erythrina mexicana	Rhizobial
Erythrina occidentalis	Rhizobial
Erythrina poeppigiana	Rhizobial
Erythrina sandwicensis	Rhizobial
Erythrina sousae	Rhizobial
Erythrina standleyana	Rhizobial
Erythrina variegata	Rhizobial
Falcataria moluccana	Rhizobial
Galactia striata	Rhizobial
Gliricidia guatemalensis	Rhizobial
Gliricidia sepium	Rhizobial
Harpalyce arborescens	Rhizobial
Harpalyce formosa	Rhizobial

Harpalyce rupicola	Rhizobial
Havardia albicans	Rhizobial
Havardia campylacantha	Rhizobial
Indigofera mucronata	Rhizobial
Indigofera palmeri	Rhizobial
Indigofera sphaerocarpa	Rhizobial
Indigofera suffruticosa	Rhizobial
Inga belizensis	Rhizobial
Inga eriocarpa	Rhizobial
Inga hintonii	Rhizobial
Inga inicuil	Rhizobial
Inga jinicuil	Rhizobial
Inga laurina	Rhizobial
Inga leptoloba	Rhizobial
Inga micheliana	Rhizobial
Inga nobilis	Rhizobial
Inga oerstediana	Rhizobial
Inga paterno	Rhizobial
Inga pavoniana	Rhizobial
Inga pringlei	Rhizobial
Inga punctata	Rhizobial
Inga radians	Rhizobial
Inga rodrigueziana	Rhizobial
Inga sapindoides	Rhizobial
Inga spuria	Rhizobial
Inga vera	Rhizobial
Inga xalapensis	Rhizobial
Inocarpus fagifer	Rhizobial
Leucaena acapulcense	Rhizobial
Leucaena collinsii	Rhizobial
Leucaena diversifolia	Rhizobial
Leucaena doylei	Rhizobial
Leucaena esculenta	Rhizobial
Leucaena glabrata	Rhizobial
Leucaena glauca	Rhizobial
Leucaena insularum	Rhizobial
Leucaena lanceolata	Rhizobial
Leucaena leucocephala	Rhizobial
Leucaena macrophylla	Rhizobial
Leucaena microcarpa	Rhizobial
Leucaena pueblana	Rhizobial
Leucaena pulverulenta	Rhizobial
Leucaena retusa	Rhizobial
Lonchocarpus acuminatus	Rhizobial
Lonchocarpus andrieuxii	Rhizobial
Lonchocarpus castilloi	Rhizobial

Lonchocarpus caudatus	Rhizobial
Lonchocarpus constrictus	Rhizobial
Lonchocarpus cruentus	Rhizobial
Lonchocarpus domingensis	Rhizobial
Lonchocarpus emarginatus	Rhizobial
Lonchocarpus eriocarinalis	Rhizobial
Lonchocarpus eriophyllus	Rhizobial
Lonchocarpus glaucifolius	Rhizobial
Lonchocarpus guatemalensis	Rhizobial
Lonchocarpus hermannii	Rhizobial
Lonchocarpus hintonii	Rhizobial
Lonchocarpus hondurensis	Rhizobial
Lonchocarpus huetamoensis	Rhizobial
Lonchocarpus lanceolatus	Rhizobial
Lonchocarpus latifolius	Rhizobial
Lonchocarpus longipedicellatus	Rhizobial
Lonchocarpus longistylus	Rhizobial
Lonchocarpus megalanthus	Rhizobial
Lonchocarpus minimiflorus	Rhizobial
Lonchocarpus obovatus	Rhizobial
Lonchocarpus parviflorus	Rhizobial
Lonchocarpus pentaphyllus	Rhizobial
Lonchocarpus punctatus	Rhizobial
Lonchocarpus robustus	Rhizobial
Lonchocarpus rugosus	Rhizobial
Lonchocarpus salvadorensis	Rhizobial
Lonchocarpus xuul	Rhizobial
Lonchocarpus yucatanensis	Rhizobial
Lysiloma acapulcense	Rhizobial
Lysiloma aurita	Rhizobial
Lysiloma bahamensis	Rhizobial
Lysiloma candida	Rhizobial
Lysiloma chiapensis	Rhizobial
Lysiloma desmostachys	Rhizobial
Lysiloma divaricatum	Rhizobial
Lysiloma latisiliquum	Rhizobial
Lysiloma microphylla	Rhizobial
Lysiloma tergemina	Rhizobial
Lysiloma thornberi	Rhizobial
Lysiloma watsonii	Rhizobial
Machaerium biovulatum	Rhizobial
Machaerium latifolium	Rhizobial
Machaerium seemanii	Rhizobial
Millettia pinnata	Rhizobial
Mimosa aculeaticarpa	Rhizobial
Mimosa albida	Rhizobial

Mimosa arenosa	Rhizobial
Mimosa bahamensis	Rhizobial
Mimosa benthamii	Rhizobial
Mimosa biuncifera	Rhizobial
Mimosa dysocarpa	Rhizobial
Mimosa ervendbergii	Rhizobial
Mimosa eurycarpa	Rhizobial
Mimosa fasciculata	Rhizobial
Mimosa galeottii	Rhizobial
Mimosa hemiendyta	Rhizobial
Mimosa invisa	Rhizobial
Mimosa lactiflua	Rhizobial
Mimosa lindheimeri	Rhizobial
Mimosa monancistra	Rhizobial
Mimosa palmeri	Rhizobial
Mimosa pigra	Rhizobial
Mimosa polyantha	Rhizobial
Mimosa pudica	Rhizobial
Mimosa purpurascens	Rhizobial
Mimosa stipitata	Rhizobial
Mimosa tenuiflora	Rhizobial
Mimosa tenuifolia	Rhizobial
Morella faya	Actinorhizal
Mucuna sloanei	Rhizobial
Myrica cerifera	Actinorhizal
Myrica mexicana	Actinorhizal
Olneya tesota	Rhizobial
Ormosia calavensis	Rhizobial
Ormosia isthmensis	Rhizobial
Ormosia krugii	Rhizobial
Ormosia macrocalyx	Rhizobial
Ormosia schippii	Rhizobial
Phaseolus vulgaris	Rhizobial
Piptadenia flava	Rhizobial
Piptadenia obliqua	Rhizobial
Piptadenia viridiflora	Rhizobial
Piscidia carthagenensis	Rhizobial
Piscidia communis	Rhizobial
Piscidia grandifolia	Rhizobial
Piscidia mollis	Rhizobial
Piscidia piscipula	Rhizobial
Piscidia sinalaensis	Rhizobial
Pisum sativum	Rhizobial
Pithecellobium acatlense	Rhizobial
Pithecellobium albicans	Rhizobial
Pithecellobium arboreum	Rhizobial

Pithecellobium belizense	Rhizobial
Pithecellobium brevifolium	Rhizobial
Pithecellobium calostachys	Rhizobial
Pithecellobium donnell-smithii	Rhizobial
Pithecellobium dulce	Rhizobial
Pithecellobium ebano	Rhizobial
Pithecellobium flexicaule	Rhizobial
Pithecellobium furcatum	Rhizobial
Pithecellobium insigne	Rhizobial
Pithecellobium keyense	Rhizobial
Pithecellobium lanceolatum	Rhizobial
Pithecellobium leiocalyx	Rhizobial
Pithecellobium leptophyllum	Rhizobial
Pithecellobium leucocalyx	Rhizobial
Pithecellobium leucospermum	Rhizobial
Pithecellobium macrosiphon	Rhizobial
Pithecellobium mangense	Rhizobial
Pithecellobium mexicanum	Rhizobial
Pithecellobium pachypus	Rhizobial
Pithecellobium pallens	Rhizobial
Pithecellobium recordii	Rhizobial
Pithecellobium sonorae	Rhizobial
Pithecellobium tortum	Rhizobial
Pithecellobium undulatum	Rhizobial
Pithecellobium unguis-cati	Rhizobial
Platymiscium dimorphandrum	Rhizobial
Platymiscium lasiocarpum	Rhizobial
Platymiscium trifoliolatum	Rhizobial
Platymiscium yucatanum	Rhizobial
Poitea florida	Rhizobial
Prosopis glandulosa	Rhizobial
Prosopis juliflora	Rhizobial
Prosopis laevigata	Rhizobial
Prosopis pallida	Rhizobial
Prosopis pubescens	Rhizobial
Prosopis spp.	Rhizobial
Prosopis velutina	Rhizobial
Pterocarpus acapulcensis	Rhizobial
Pterocarpus hayesii	Rhizobial
Pterocarpus indicus	Rhizobial
Pterocarpus marsupium	Rhizobial
Pterocarpus officinalis	Rhizobial
Pterocarpus orbiculatus	Rhizobial
Pterocarpus rohrii	Rhizobial
Robinia neomexicana	Rhizobial
Robinia pseudoacacia	Rhizobial

Samanea saman	Rhizobial
Sophora affinis	Rhizobial
Sophora chrysophylla	Rhizobial
Sophora conzattii	Rhizobial
Sophora nuttalliana	Rhizobial
Sophora secundiflora	Rhizobial
Swartzia cubensis	Rhizobial
Swartzia ochnacea	Rhizobial
Swartzia simplex	Rhizobial
Tephrosia palmeri	Rhizobial
Vigna adenantha	Rhizobial
Zygia corata	Rhizobial
Zygia stevensonii	Rhizobial

Table S2. Higher and lower latitude relative abundance means for all N-fixers. *P*-values for all Tukey HSD tests for post-hoc differences between latitude-scale higher and lower latitudes are significant at $P < 0.02$. Tukey HSD significant differences for island groups vs. latitude-scale lower latitudes are marked with * ($P < 0.05$).

Fit	Lower latitude		Higher latitude		Islands	
Scale:	Plot	Latitude	Plot	Latitude	Plot	Island group
% basal area, 30°	13.1	11.3	1.8	4.3	16.9	11.7
% basal area, 32°	11.6	12.4	1.4	2.9	16.9	11.7
% basal area, 34°	10.6	13.2	0.9	1.3	16.9	11.7
% basal area, 35°	9.1	12.7	0.8	1.2	16.9	11.7
% basal area, 36°	8.0	12.4	0.8	0.9	16.9	11.7
% basal area, 38°	6.2	11.5	0.8	0.9	16.9	11.7
% basal area, 40°	5.4	10.8	0.4	0.7	16.9	11.7
% individuals, 30°	9.9	12.6	1.3	4.7	16.9	6.7
% individuals, 32°	6.4	13.6	1.2	3.3	16.9	6.7
% individuals, 34°	5.1	14.3	0.9	1.7	16.9	6.7*
% individuals, 35°	4.3	13.9	0.9	1.5	16.9	6.7*
% individuals, 36°	3.7	13.6	0.9	1.2	16.9	6.7
% individuals, 38°	3.2	12.6	0.8	1.2	16.9	6.7
% individuals, 40°	3.0	11.8	0.4	1.0	16.9	6.7

Table S3. Taxonomic richness for a standardized area in each degree of latitude or island group. P-values for all Tukey HSD tests for post-hoc differences between latitude-scale higher and lower latitudes are significant at $P < 0.05$ except for actinorhizal genera with a 40° cutoff ($P = 0.051$).

Fit	Lower latitude means				Higher latitude means				Island means			
	All fix	Rhiz	Act	Trees	All fix	Rhiz	Act	Trees	All fix	Rhiz	Act	Trees
Genera												
30°	30.6	27.2	3.4	301	3.4	1.6	1.9	41.1	20.9	18.8	2.1	261
32°	27.9	24.7	3.2	275	3.2	1.3	1.9	39.2	20.9	18.8	2.1	261
34°	25.8	22.7	3.1	253	2.9	1.0	1.9	37.3	20.9	18.8	2.1	261
35°	24.8	21.8	3.0	244	2.8	0.9	1.9	36.4	20.9	18.8	2.1	261
36°	23.9	20.9	3.0	235	2.6	0.8	1.9	35.2	20.9	18.8	2.1	261
38°	22.2	19.4	2.9	220	2.5	0.6	1.9	33.0	20.9	18.8	2.1	261
40°	20.9	18.0	2.8	208	2.3	0.4	1.9	30.0	20.9	18.8	2.1	261
Species												
30°	93.1	86.8	6.3	697	4.8	2.3	2.6	123	28.4	25.9	2.5	369
32°	83.8	78.0	5.8	642	4.4	1.8	2.6	116	28.4	25.9	2.5	369
34°	76.5	71.1	5.5	598	3.9	1.2	2.6	108	28.4	25.9	2.5	369
35°	73.3	67.9	5.3	579	3.7	1.0	2.7	104	28.4	25.9	2.5	369
36°	70.3	65.1	5.3	561	3.4	0.9	2.6	99.4	28.4	25.9	2.5	369
38°	65.0	59.9	5.1	530	3.1	0.6	2.6	90.0	28.4	25.9	2.5	369
40°	60.4	55.4	5.0	503	2.8	0.4	2.4	78.0	28.4	25.9	2.5	369

Table S4. Relative taxonomic richness for each degree of latitude or island group. *P*-values for all Tukey HSD tests for post-hoc differences between latitude-scale higher and lower latitudes are significant at $P < 0.05$ except for all fixer genera with a 40° cutoff *(*$P = 0.088$). Island means are not significantly different from lower latitude means for all genus-level comparisons.

Fit	Lower latitude means			Higher latitude means			Island means		
	All fix	Rhiz	Act	All fix	Rhiz	Act	All fix	Rhiz	Act
% Genera									
30°	11.2	9.8	1.4	8.2	2.8	5.4	8.3	7.3	1.0
32°	11.0	9.5	1.4	8.1	2.5	5.7	8.3	7.3	1.0
34°	11.1	9.5	1.7	7.8	1.9	5.9	8.3	7.3	1.0
35°	11.0	9.3	1.7	7.7	1.7	6.0	8.3	7.3	1.0
36°	10.9	9.1	1.8	7.7	1.5	6.1	8.3	7.3	1.0
38°	10.6	8.7	1.9	7.7	1.3	6.4	8.3	7.3	1.0
40°	10.3	8.2	2.1	7.8	1.1	6.7	8.3	7.3	1.0
% Species									
30°	13.1	12.0	1.1	4.7	1.2	3.4	7.7	6.9	0.8
32°	12.1	11.1	1.0	4.7	1.0	3.7	7.7	6.9	0.8
34°	11.5	10.4	1.1	4.6	0.7	3.9	7.7	6.9	0.8
35°	11.1	10.1	1.0	4.6	0.6	4.0	7.7	6.9	0.8
36°	10.8	9.7	1.1	4.7	0.6	4.1	7.7	6.9	0.8
38°	10.2	9.0	1.1	4.8	0.4	4.4	7.7	6.9	0.8
40°	9.6	8.4	1.2	5.0	0.4	4.7	7.7	6.9	0.8

Table S5. Fits for relative abundance against relative richness.

Fit		Slope (95% CIs)		Slope ratio	
Latitude:	Lower	Higher	Islands	H/L	I/L
All N-fixing trees					
% basal area ~ % genera	1.11 (0.11)	0.12 (0.14)	1.46 (0.24)	0.10	1.32
% individuals ~ % genera	1.20 (0.10)	0.15 (0.14)	0.88 (0.39)	0.13	0.73
% basal area ~ % species	0.97 (0.12)	0.13 (0.24)	1.69 (0.32)	0.13	1.74
% individuals ~ % species	1.08 (0.12)	0.16 (0.24)	1.15 (0.44)	0.15	1.06
% basal area ~ % genera, 34°	1.12 (0.11)	0.14 (0.14)	1.46 (0.24)	0.12	1.30
% basal area ~ % genera, 36°	1.10 (0.11)	0.09 (0.14)	1.46 (0.24)	0.08	1.33
Rhizobial N-fixing trees					
% basal area ~ % genera	1.26 (0.13)	0.31 (0.51)	1.64 (0.27)	0.25	1.30
% individuals ~ % genera	1.35 (0.13)	0.33 (0.50)	0.97 (0.35)	0.24	0.72
% basal area ~ % species	1.00 (0.13)	1.00 (1.54)	1.84 (0.35)	1.00	1.84
% individuals ~ % species	1.10 (0.13)	1.05 (1.56)	1.27 (0.53)	0.96	1.16
% basal area ~ % genera, 34°	1.27 (0.13)	0.40 (0.44)	1.64 (0.27)	0.32	1.29
% basal area ~ % genera, 36°	1.26 (0.12)	0.12 (0.54)	1.64 (0.27)	0.09	1.29
Actinorhizal N-fixing trees					
% basal area ~ % genera	0.09 (0.09)	0.07 (0.02)	0.40 (0.27)	0.81	4.63
% individuals ~ % genera	0.22 (0.13)	0.10 (0.04)	0.36 (0.42)	0.44	1.65
% basal area ~ % species	0.22 (0.16)	0.07 (0.03)	0.52 (0.34)	0.30	2.37
% individuals ~ % species	0.55 (0.24)	0.09 (0.05)	0.50 (0.54)	0.17	0.91
% basal area ~ % genera, 34°	0.10 (0.09)	0.07 (0.02)	0.40 (0.27)	0.72	4.15
% basal area ~ % genera, 36°	0.09 (0.08)	0.07 (0.02)	0.40 (0.27)	0.75	4.35

Figures

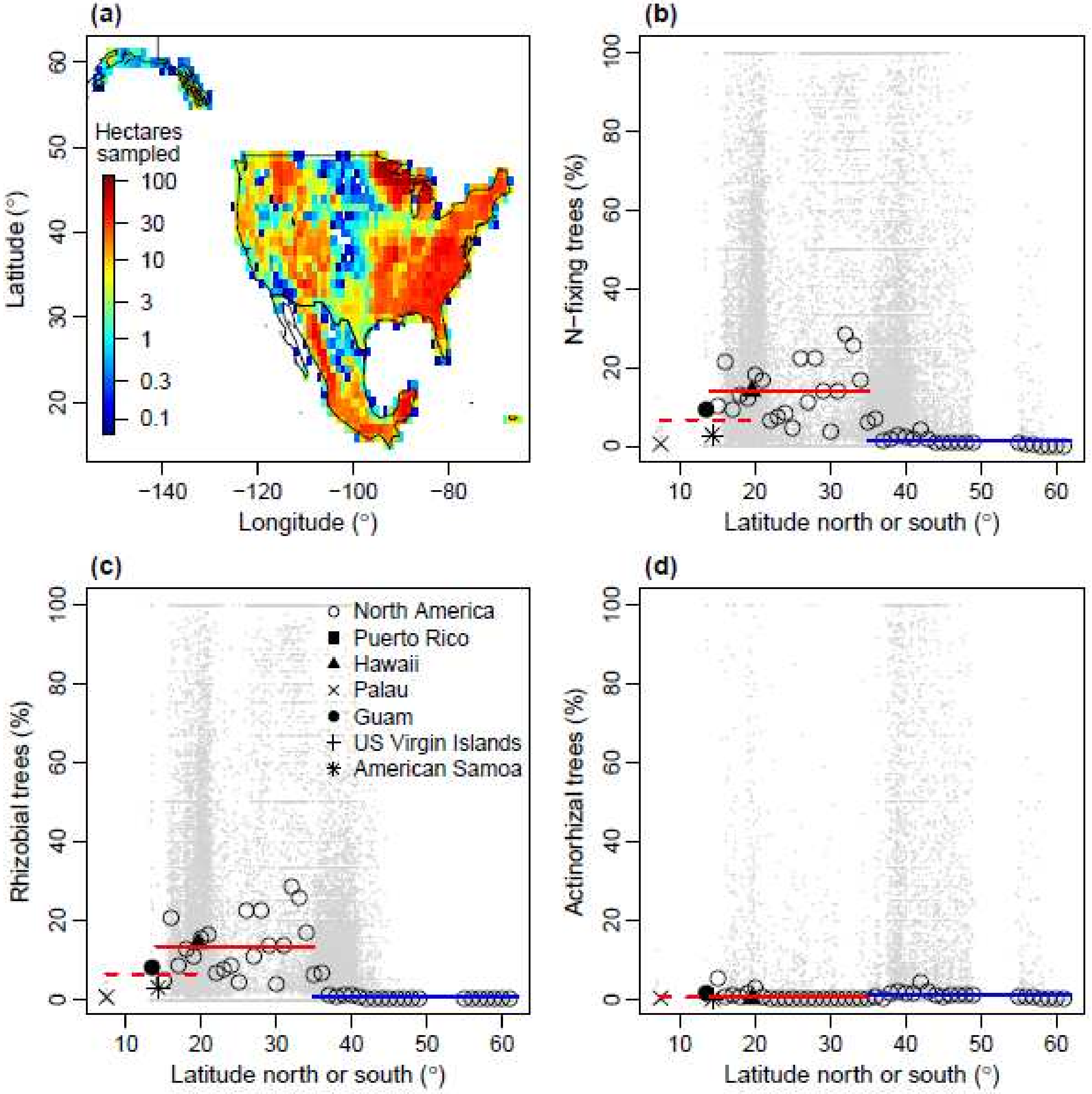


Figure S1. Nitrogen (N)-fixing tree relative abundance across latitude for proportion of individual trees. All details for Fig. S1a are the same as for Fig. 2a except that the color scale is plot area instead of the number of plot records. Area sampled is calculated for the standard subplots (not macroplots) used to sample adult trees. Each unique plot location was included once in our area calculations, regardless of how many times a plot was measured. All details for Fig. S1b-d are the same as in Fig. 2b-d except that the vertical axis is the proportion of individuals instead of the proportion of basal area, and that plot-level values are also shown (small gray dots).

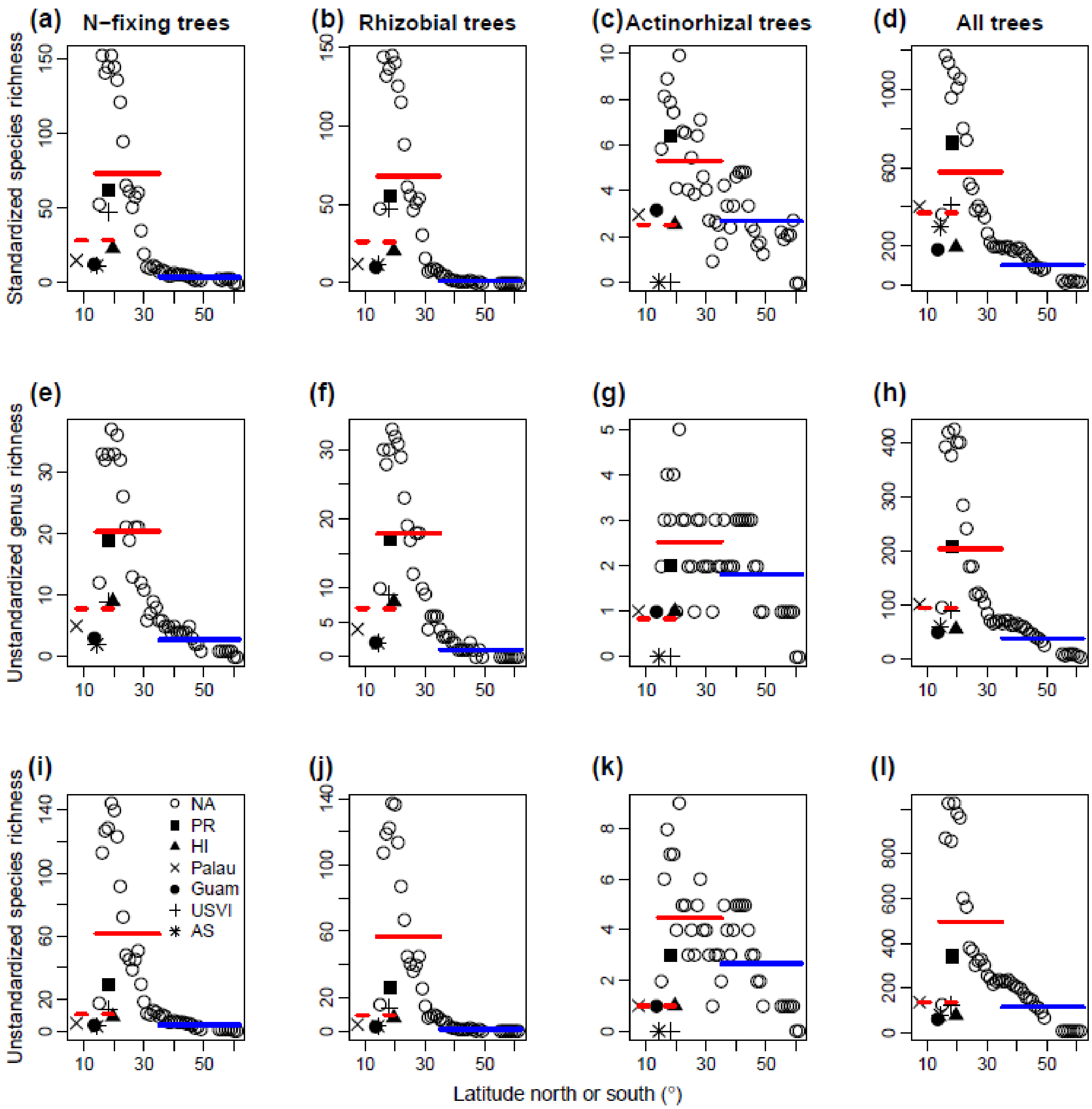


Figure S2. N-fixing tree taxonomic richness across latitude. Details follow Fig. 3, except for the following differences. Panels (a)-(d) show species richness instead of genus richness. Genus richness (e)-(h) and species richness (i)-(l) are also shown uncorrected for different sampling areas. In panels (e)-(l), each point is the number of taxa in all records in a given 1° latitude. Legend abbreviations are NA: North America; PR: Puerto Rico; HI: Hawaii; USVI: US Virgin Islands, and AS: American Samoa.

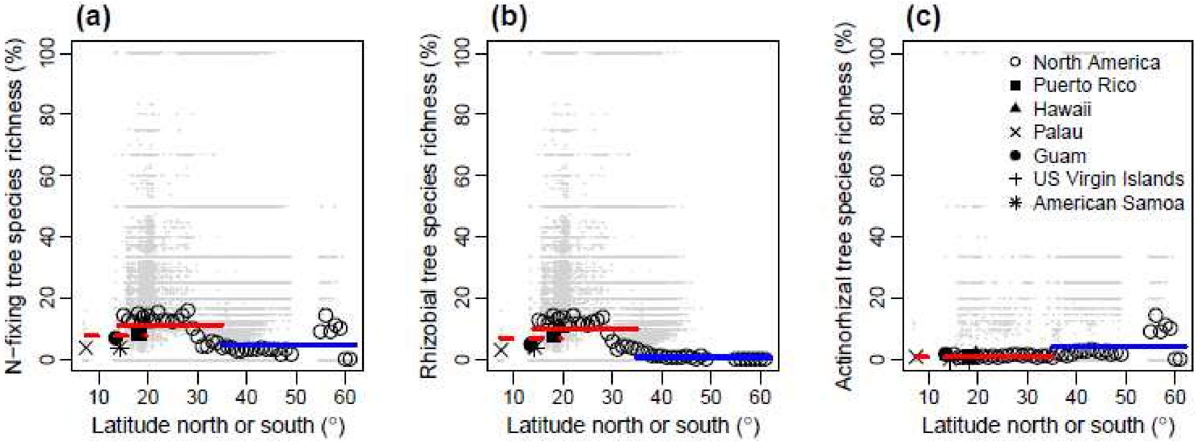


Figure S3. N-fixing tree relative taxonomic richness across latitude. Details follow Fig. 4, except that the vertical axis is the percent of species instead of genera and that plot-level values are also shown (small gray dots).

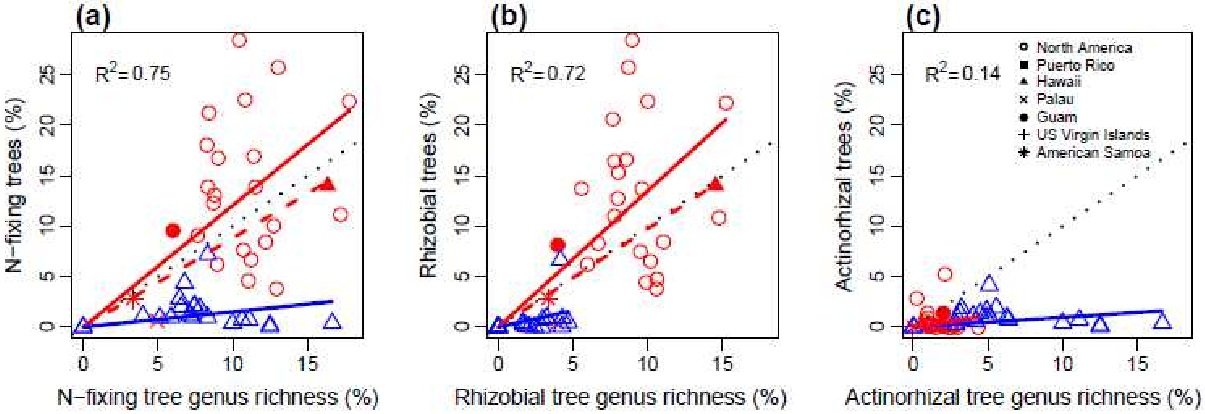


Figure S4. N-fixing tree relative individual abundance as a function of relative genus richness. This figure is the same as Fig. 5 except that the vertical axis is % individual trees instead of % basal area.

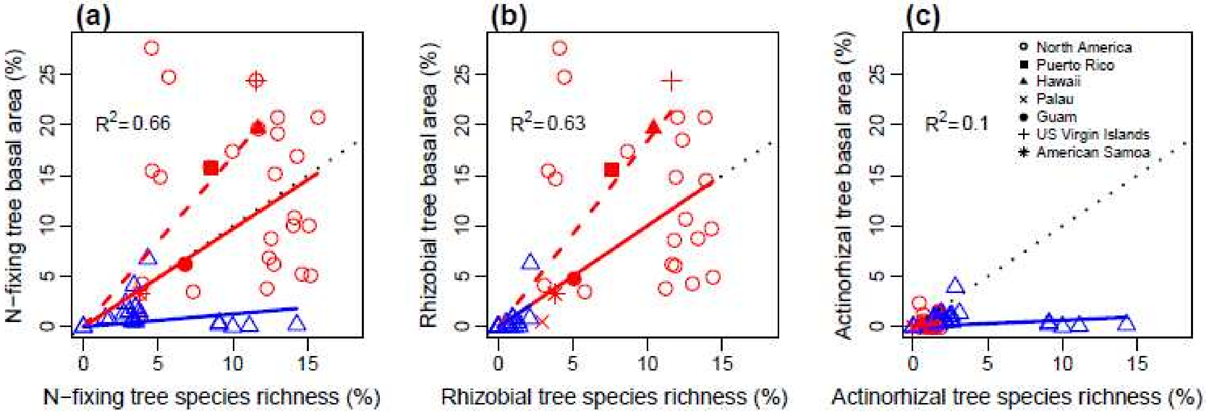


Figure S5. N-fixing tree relative basal area as a function of relative species richness. This figure is the same as Fig. 5 except that the horizontal axis is % species instead of % genera.

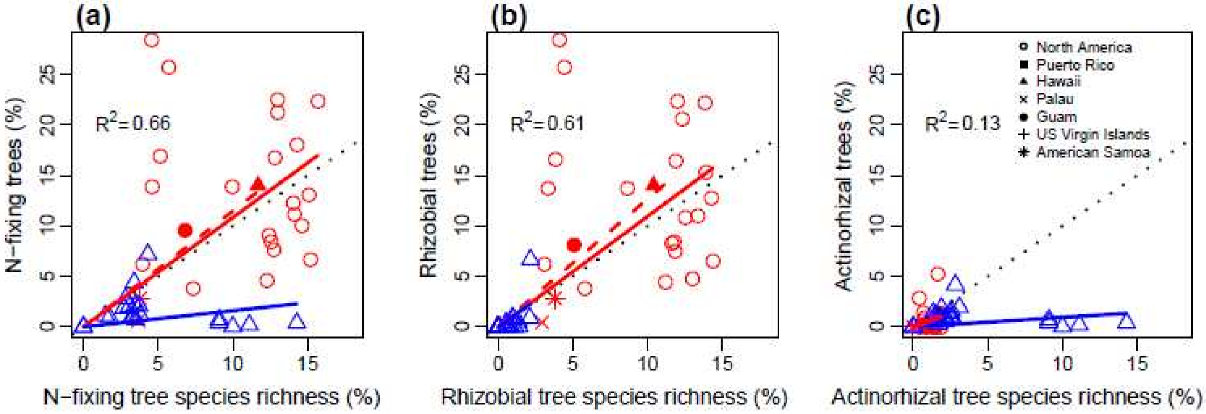


Figure S6. N-fixing tree relative individual abundance as a function of relative species richness. This figure is the same as Fig. 5 except that the vertical axis is % individual trees instead of % basal area, and the horizontal axis is % species instead of % genera.

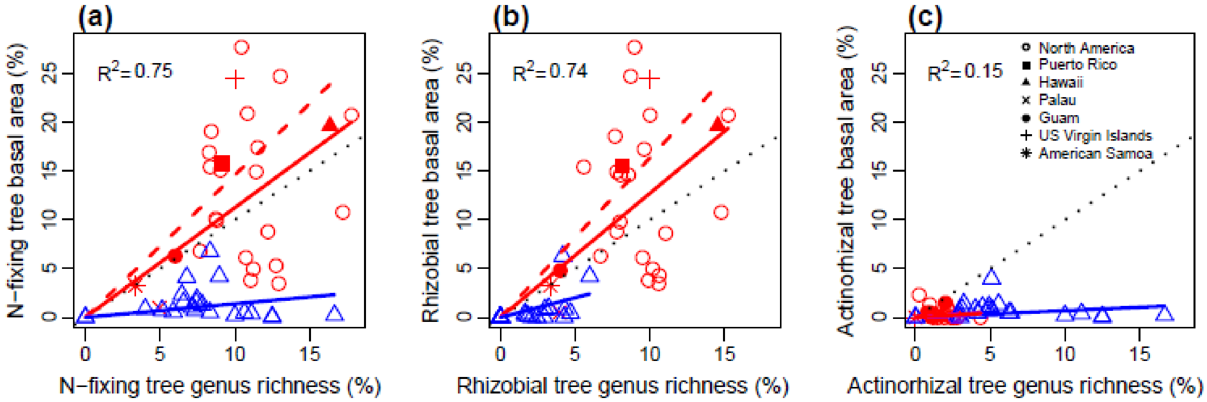


Figure S7. N-fixing tree relative basal area as a function of relative genus richness for a 34° latitude cutoff. This figure is the same as Fig. 5 except that the latitude cutoff to divide higher-latitude from lower-latitude data is 34° instead of 35°.

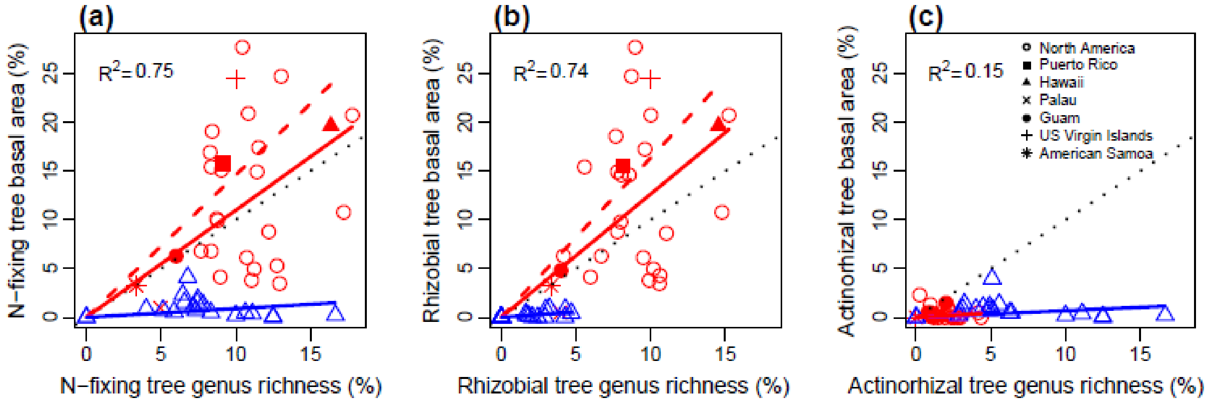


Figure S8. N-fixing tree relative basal area as a function of relative genus richness for a 36° latitude cutoff. This figure is the same as Fig. 5 except that the latitude cutoff to divide higher-latitude from lower-latitude data is 36° instead of 35°.