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RESEARCH ARTICLE

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Patterns of nitrogen-fixing tree abundance in forests across Asia and America

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Abstract

1. Symbiotic nitrogen (N)-fixing trees can provide large quantities of new N to ecosystems, but only if they are sufficiently abundant. The overall abundance and latitudinal abundance distributions of N-fixing trees are well characterised in the Americas, but less well outside the Americas.
2. Here, we characterised the abundance of N-fixing trees in a network of forest plots spanning five continents, ~5,000 tree species and ~4 million trees. The majority of the plots (86%) were in America or Asia. In addition, we examined whether the observed pattern of abundance of N-fixing trees was correlated with mean annual temperature and precipitation.
3. Outside the tropics, N-fixing trees were consistently rare in the forest plots we examined. Within the tropics, N-fixing trees were abundant in American but not Asian forest plots (~7% versus ~1% of basal area and stems). This disparity was not explained by mean annual temperature or precipitation. Our finding of low N-fixing tree abundance in the Asian tropics casts some doubt on recent high estimates of N fixation rates in this region, which do not account for disparities in N-fixing tree abundance between the Asian and American tropics.
4. *Synthesis*. Inputs of nitrogen to forests depend on symbiotic nitrogen fixation, which is constrained by the abundance of N-fixing trees. By analysing a large dataset of ~4 million trees, we found that N-fixing trees were consistently rare in the Asian tropics as well as across higher latitudes in Asia, America and Europe. The rarity of N-fixing trees in the Asian tropics compared with the American tropics might stem from lower intrinsic N limitation in Asian tropical forests, although direct support for any mechanism is lacking. The paucity of N-fixing trees throughout Asian forests suggests that N inputs to the Asian tropics might be lower than previously thought.

KEYWORDS
forest, legume, nitrogen fixation, nutrient limitation, Smithsonian ForestGEO, symbiosis

1 | INTRODUCTION

Symbiotic nitrogen (N)-fixing trees play pivotal ecological and biogeochemical roles. They can bring over 100 kg N ha^{-1} $year^{-1}$ into ecosystems (Binkley, Cromack, & Baker, 1994), which can fuel rapid forest growth and carbon sequestration (Batterman, Hedin, et al., 2013). However, they can also inhibit forest growth (Chapin, Conway, Johnstone, Hollingsworth, & Hollingsworth, 2016; Taylor, Chazdon, Bachelot, & Menge, 2017), presumably by taking light or other resources away from their neighbors. Additionally, when N is already available in excess, N fixation can exacerbate N export (Compton, Church, Larned, & Hogsett, 2003; Erickson & Perakis, 2014), with potentially global consequences (Kou-Giesbrecht & Menge, 2019). Nitrogen can be exported as nitrate (Compton et al., 2003), which degrades water quality and causes eutrophication; as nitrous oxide (Erickson & Perakis, 2014), which exacerbates atmospheric warming; or as nitric oxide (Erickson & Perakis, 2014), which causes local air pollution.

According to systematic government forest inventories from the USA, Mexico and Amazonia (Menge, Batterman, Liao, et al., 2017; Menge, Lichstein, & Ángeles-Pérez, 2014; ter Steege et al., 2006), N-fixing trees comprise ~10% of tree basal area from the tropics to 35°N, where they survive better (Menge & Chazdon, 2016) and grow faster (Batterman, Hedin, et al., 2013; Menge & Chazdon, 2016) than non-fixing trees in early succession, and hence often persist late into succession (Gei et al., 2018). In contrast, N-fixing trees comprise <1% of tree basal area (Menge, Batterman, Liao, et al., 2017; Menge et al., 2014) north of 35°N in the USA, where they grow slower and have a higher mortality than non-fixing trees (Liao & Menge, 2016), and hence are confined to early succession (Chapin, Walker, Fastie, & Sharman, 1994; Menge, DeNoyer, & Lichstein, 2010). N-fixing organisms other than trees (symbiotic shrubs, herbs and lianas; moss- and lichen-associated cyanobacteria; and free-living bacteria) also bring new N into ecosystems (Reed, Cleveland, & Townsend, 2011) and constitute a major part of the biota at higher latitudes (Sprent, 2009). However, our focus here is on symbiotic N-fixing trees, which are tree taxa that can form N-fixing symbioses, regardless of whether they are actively symbiotic. N-fixing tree taxa consist of rhizobial taxa (many but not all legumes, i.e., taxa in the family Fabaceae, and the genus *Parasponia*, in the family Cannabaceae, which form symbioses with *Rhizobia*-type bacteria) and actinorhizal taxa (twenty-six genera from eight other families—Betulaceae, Casuarinaceae, Coriariaceae, Datiscaceae, Elaeagnaceae, Myricaceae, Rhamnaceae and Rosaceae—that form symbioses with *Frankia*-type bacteria; Huss-Danell, 1997). The abundance of trees from these taxa is a measure of their capacity for N fixation and thus their ability to respond to increased N demand, although it does not indicate their realised rate of N fixation (Taylor, Chazdon, & Menge, 2019).

Why are N-fixing trees an order of magnitude more abundant at lower latitudes than at higher latitudes in the Americas? One hypothesis posits that the biogeography of woody legumes confines N-fixing trees to the tropics (Crews, 1999), although the generally strong positive correlations in tree family abundances across continents (Etienne & Rosindell, 2012), the preponderance of extratropical herbaceous legumes (Sprent, 2009), the fact that N-fixing trees comprise a similar fraction of tree taxa across latitude (Menge, Batterman, Liao, et al., 2017), the altitudinal patterns of N-fixing tree abundance in the tropics (Menge et al., 2014), and a model of trait evolution (Menge & Crews, 2016) all suggest that biogeography is not the driver. A second hypothesis proposes that N fixation is favored in warm environments, and that fixed N can be invested in mechanisms to alleviate the phosphorus limitation that is relatively strong in the tropics (Houlton, Wang, Vitousek, & Field, 2008). Although some studies have found that N fixers have higher phosphatase activity (Nasto et al., 2014,2017; Png et al., 2017), other studies have not (Batterman et al., 2018; Batterman, Wurzburger, & Hedin, 2013; Soper, Nasto, Osborne, & Cleveland, 2018), and recent work calls into question the logic that such a link would lead to higher N-fixer abundance in low P soils (Batterman et al., 2018). A third hypothesis is that lower-latitude N-fixing trees are better able than higher-latitude N-fixing trees to regulate N fixation based on their degree of N limitation relative to other resources (Menge et al., 2014), which might have resulted from the effects of warmer temperatures on soil N cycling (Sheffer, Batterman, Levin, & Hedin, 2015). A fourth hypothesis states that severe N limitation—where N demand far exceeds soil N supply, such that N fixation is cost-effective—is more common at lower latitudes (Menge, Batterman, Hedin, et al., 2017). One way to evaluate such hypotheses is to study latitudinal patterns of N-fixing trees in both the Americas and other continents. If climate is the ultimate driver, for example, N-fixing tree abundance should mirror how climate varies among continents.

Although no study to date has evaluated N-fixing tree abundance on a broad geographic scale outside the Americas, previous studies have evaluated the abundance of legume trees. Because many legume trees are N-fixers, these studies might indicate the pattern of N-fixing trees. Gentry's classic studies used 0.1 ha plots to compare the abundance and diversity of legumes in different biogeographic regions (Gentry, 1982, 1988, 1993). Gentry found that, in terms of abundance and species richness, legumes often dominated other plant families in forests in the Neotropics and tropical Africa (Gentry, 1988, 1993). In contrast, the relative number of legume species in Southeast Asia was lower than in the Neotropics and tropical Africa (Gentry, 1988), although he had many fewer plots in Southeast Asia than in the Neotropics. A recent study (Lu & Hedin, 2019) classified the taxa in Gentry's plots by N-fixing status, but did not report patterns across continents. A study from the Center for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO) network—a network of large, mainly mature forest plots—showed that on average, legumes had a higher relative abundance in three plots in tropical Africa than in four plots in tropical America, which in turn had a higher relative abundance of legumes than in nine plots in tropical Asia (Losos & Leigh, 2004). A later study (Yahara et al., 2013) using more CTFS-ForestGEO plots found similar trends: On average, legumes were most abundant in Africa (11.1% of trees and 49% of basal area, from 5 plots), of intermediate abundance in America (4.7% of trees and 7.4% of basal area, from 5 plots), and comparatively rare in Asia (2.6% of trees and 2.5% of basal area, from 17 plots). Although these studies established the patterns of legume trees in different

biogeographic regions, they did not reveal the patterns of N-fixing trees because many legumes are incapable of N fixation (Sprent, 2009) and many non-legumes (*Parasponia* and actinorhizal species) are N-fixers. Furthermore, they do not reveal how the latitudinal trends compare on different continents. In Yahara et al. (2013), for example, all 10 plots in Africa and America are tropical, whereas some of the Asian plots are temperate. Conceivably, therefore, the lower abundance of legumes reported for the Asian plots could simply result from a higher proportion of extratropical plots in Asia.

Here, we analysed data from a large set of CTFS-ForestGEO plots (44 as opposed to 16 in Losos and Leigh (2004) and 27 in Yahara et al. (2013)) that span latitudinal gradients in the Americas and Asia, as well as parts of Europe and Oceania. With these data, we addressed the following questions: (Q1) How abundant and diverse are N-fixing trees compared to non-fixing trees in tropical forests among different continents? (Q2) How do latitudinal trends of the abundance and diversity of N-fixing trees differ between Asia and America? In addition, to investigate potential drivers of the patterns of diversity and abundance of N-fixing trees, we addressed the following questions: (Q3) How do growth, mortality, and recruitment of N-fixing trees compare with those of non-fixing trees among continents and across latitude? (Q4) How does the abundance of N-fixing trees vary with climate in Asia and America? Given the limitations of existing datasets, we could not examine N limitation or other soil properties directly. However, because N limitation is thought to be critical to the success of N-fixing trees, we used a dynamic model to address the question: (Q5) What patterns of N limitation could explain the differences in N-fixing tree abundance between Asia and America?

2 | MATERIALS AND METHODS

2.1 | Sites and tree censuses

We used tree census data from 44 plots in the Center for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO) long-term monitoring network, which consists of large forest plots spread across five continents (Anderson-Teixeira et al., 2015; Bunyavejchewin, Baker, LaFrankie, & Ashton, 2001; Bunyavejchewin, LaFrankie, Baker, Davies, & Ashton, 2009; Bunyavejchewin et al., 1998; Condit, 1998; Dandois et al., 2015; Furniss, Larson, & Lutz, 2017; Hubbell, Condit, & Foster, 2015; Hubbell et al., 1999; Janík et al., 2016; Lee et al., 2002, 2005; Lutz, Larson, Freund, Swanson, & Bible, 2013; Lutz et al., 2014; Lutz, Larson, Swanson, & Freund, 2012; Manokaran & LaFrankie, 1990; Spasojevic, Yablon, Oberle, & Myers, 2014; Vincent, Henning, Saulei, & Sosanika, 2015) (http://www.forestgeo.si.edu/). In each plot, all free-standing woody stems ≥1 cm diameter-at-breast-height (DBH; 1.3 m) are tagged, identified to the lowest taxonomic level possible (usually species) and measured, with re-censuses at intervals of typically 5 years (Anderson-Teixeira et al., 2015). Our study included 19, 19, 3 and 3 plots from America (North, Central and South America), Asia, Europe and Oceania (Hawaii and Papua New Guinea), respectively (Figure 1 and Figure S1 in Appendix S1). Of these plots, 24 have data from more than one census (two to six censuses); the remaining 20 have data from only one census (Figure 1, Figure S1). The plots span a latitudinal gradient from −2.4 to 52.3° (1.4–40.0° for the Asian plots, −2.4 to 45.8° for the American plots). The sizes of the plots range from 2 to 60 ha (mean = 24.6 ha, median = 25 ha). We excluded fern and palm species from our analyses because their life-histories and/or growth patterns can be very different than other woody species. The number of tree species differs among the plots by two orders of magnitude, from 11 to 1,330, and generally decreases from the tropics to the poles (Appendix S2; Ricklefs & He, 2016).

The 44 plots we examined include many tropical rainforests on upland or *terra firme* habitats, as well as temperate forests in eastern North America and China. Because our plots only include one tropical dry forest (the Mudumalai plot in Asia), we restrict our conclusions about tropical forests to tropical rainforests. In general, the 44 plots we examined are old growth or mature secondary forests that are well-protected (Anderson-Teixeira et al., 2015). For 41 of these 44 plots, Anderson-Teixeira et al. (2015) calculated a 'degradation index' for the area around the plots, which suggested that natural and anthropogenic disturbances have generally not had major effects on forests in the areas surrounding the plots. Appendix S2 summarises the key statistics for each of the 44 plots examined, including location and climate, and the abundance and diversity of the tree community.

Our dataset includes more plots in tropical Asia (15 plots) than tropical America (6 plots) and more plots in extratropical America (13 plots) than extratropical Asia (4 plots), but these sampling asymmetries do not strongly influence our conclusions, for two reasons. First, our American results largely match findings from government forest inventories in the USA and Mexico (Liao & Menge, 2016; Liao, Menge, Lichstein, & Ángeles-Pérez, 2017; Menge, Batterman, Liao, et al., 2017; Menge et al., 2014), as well as Amazonia (ter Steege et al., 2006). Second, our results from tropical Asia, which is the region that diverges most from our prior expectations, have strong support because it is the best sampled region in our analysis.

2.2 | N-fixing taxa and diversity metrics

For 43 of the 44 plots, we classified taxa as capable or incapable of forming N-fixing symbioses based on published reports (Huss-Danell, 1997; Sprent, 2009). Because N fixation is essentially a genus-level trait (Huss-Danell, 1997; Sprent, Ardley, & James, 2017) and many species have not been examined for the capacity to form N-fixing symbioses, we classified a plant species as a rhizobial N-fixer if its genus was listed in Sprent (2009) and as an actinorhizal N-fixer if its genus was listed in Huss-Danell (1997) or its genus was *Morella* (which was split from *Myrica* after 1997). We classified individuals of unknown taxonomic origin as non-fixers, but these make up only a tiny fraction of the total number of individuals. Appendix S3 lists all the species we classified as N-fixing. For the remaining plot (Kuala Belalong), local taxonomic experts determined that all the legumes can form N-fixing symbioses but no other tree taxa can. Importantly, our classification concerns the potential to fix N, not rates of N fixation, which require much more detailed process-level work than can currently be achieved at the scale of the CTFS-ForestGEO network.

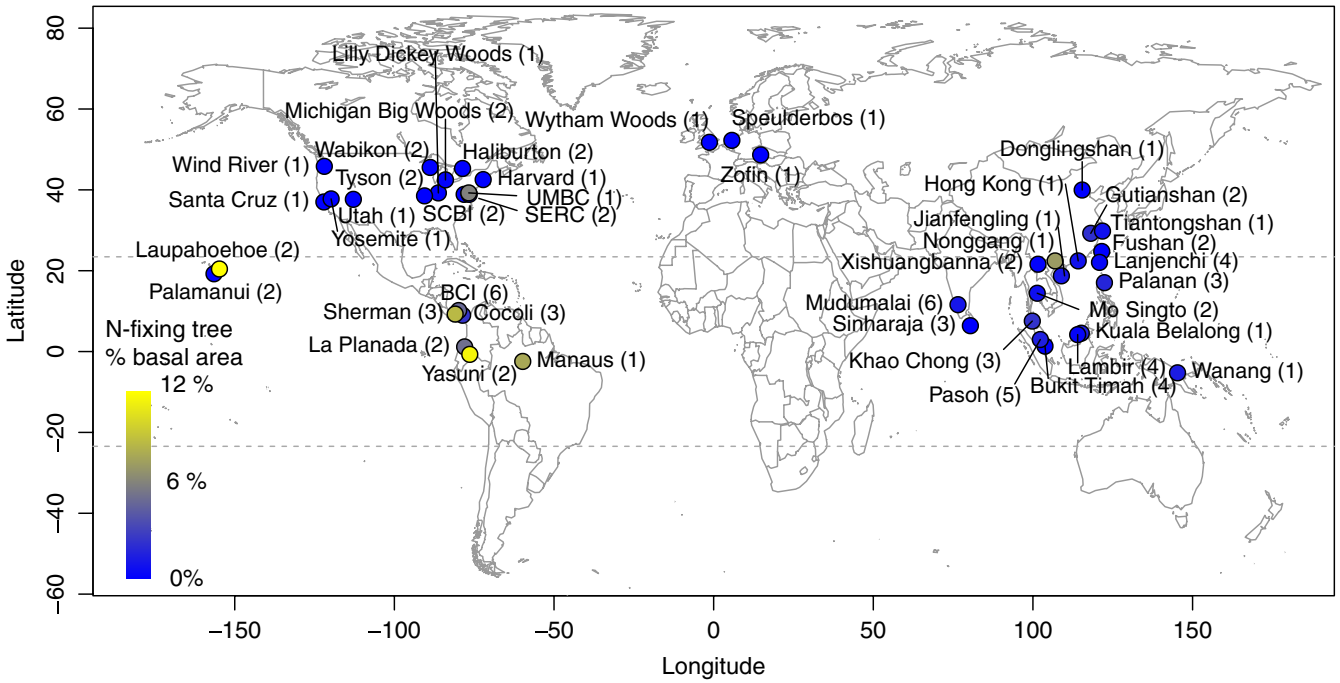

FIGURE 1 Map showing locations and N-fixing tree abundances of the 44 CTFS-ForestGEO plots. Each plot is represented by a circle, together with its name and the number of censuses (in parentheses). UMBC, SCBI, SERC and BCI stand for University of Maryland, Baltimore County; Smithsonian Conservation Biology Institute; Smithsonian Environmental Research Center; and Barro Colorado Island respectively. Plot colour indicates the % of total tree basal area from N-fixing trees (see color bar), except that Laupahoehoe (20.5%) is off the color scale and is assigned the color corresponding to the highest value on the scale. The three plots in Panama and two plots in Hawaii are offset slightly for visual clarity. Dashed grey lines indicate the Tropics of Cancer and Capricorn, which are the lines used to divide tropical and extratropical plots [Colour figure can be viewed at wileyonlinelibrary.com]

Rates of N fixation vary considerably across taxa (Wurzburger & Hedin, 2016) and environmental conditions (Barron, Purves, & Hedin, 2011; Batterman, Hedin, et al., 2013).

The diversity of N-fixing trees in a forest plot can be quantified either as an absolute value or as a relative value (e.g., a fraction of total tree diversity). Relative measures are more useful for comparing N-fixing to non-fixing trees across plots that differ in total tree abundance and total diversity. Therefore, in our study, we focus on relative values of N-fixing tree diversity, although we also present absolute values in Appendix S1.

As absolute measures of diversity of N-fixing trees, we examined species and genus richness of N-fixing trees per unit area of each plot. As relative measures of diversity of N-fixing trees, which account for different sample sizes and different total tree diversities at each plot, we examined species and genus richness of N-fixing trees expressed as proportions of the total species and genus richness of trees respectively. For plots with more than one census, we took the arithmetic mean of diversity values across censuses to produce a single summary statistic for each plot and diversity metric. For the Bukit Timah plot (Singapore), we used only data from the 2 ha primary forest section of the 4 ha plot. We also calculated relative species richness and relative genus richness using the census data rarefied by sample size (Hurlbert, 1971) and sample coverage (Chao & Jost, 2012), which gave values that were very similar to the unrarefied versions (Appendix S2; the few NA values for each metric refer to plots for which insufficient data were available for rarefaction). Therefore, we report only results for the unrarefied versions in the main text.

2.3 | Calculating abundances and demographic rates

Similar to diversity, the abundance of N-fixing trees in a plot can be quantified either as an absolute value or as a relative value. As we did for the diversity of N-fixing trees, we focus on relative measures because they facilitate comparison of N-fixing trees to non-fixing trees across plots that differ in total tree abundance. However, we also calculate and present absolute values in Appendix S1, which are more useful for inferring N fixation potential over a given area.

For each census in a plot, as our first measure of absolute N-fixing tree abundance, we calculated the number of live N-fixing main stems and divided by the area of the plot. In plots where the main stems were not indicated, we assumed that the main stem was the one with the largest DBH. Abundance measured as the number of main stems does not capture the size structure of a forest, so for each census in a plot, as our second measure of absolute N-fixing tree abundance, we calculated the N-fixing tree basal area and divided by the area of the plot. The basal area of a tree was estimated as the basal area of the main stem, which was calculated as $\pi(\mathrm{DBH}/2)^2$. In addition, for each census in a plot, we calculated two measures of relative N-fixing tree abundance. The first measure was the relative number of N-fixing main stems, which we calculated as

the number of live N-fixing main stems divided by the total number of live main stems (non-fixing and N-fixing). The second measure was the relative basal area of N-fixing trees, which we calculated as the N-fixing tree basal area divided by the total tree basal area. For plots with more than one census, we took the arithmetic mean of abundances across censuses to produce a single summary statistic for each plot and abundance metric. Basal area for the Huai Kha Khaeng plot (Thailand) could not be calculated because of lack of access to DBH data. As for relative taxonomic richness, we also calculated the relative number of stems and basal area using the census data rarefied by sample size and sample coverage, and found that these were very similar to the unrarefied versions (Appendix S2; the few NA values for each metric refer to plots for which insufficient data were available for rarefaction). Therefore, we report results only for the unrarefied versions in the main text.

Demographic rates could be calculated only for plots with more than one census. For abundance measured as the number of main stems, we calculated the instantaneous mortality rate over two censuses as $m = [\ln(N_0) - \ln(S)]/\Delta T$, where N_0 is the number of stems in the first census, S is the number of survivors from the first to the second census, and ΔT is the length of time between the censuses measured in years (Condit et al., 2006). Because the time between censuses differs from stem to stem, we computed ΔT as the average time over all the stems within a plot and census interval. The expression for m was derived from the differential equation $dN/dt = -mN$, as explained in Condit et al. (2006). Similarly, we calculated the instantaneous recruitment rate over two censuses as $r = [\ln(N_0 + R) - \ln(N_0)]/\Delta T$, where R is the number of stems appearing in the second census for the first time. The instantaneous growth rate was calculated as $g = [\ln(A_0 + G) - \ln(A_0)]/\Delta T$, where A_0 is the basal area in the first census and G is the increase in basal area of surviving trees in between the two censuses. All rates were computed for both non-fixers and N-fixers. For each plot with more than two censuses, apart from the Huai Kha Khaeng plot, we calculated each rate for every pair of consecutive censuses and took the arithmetic mean to produce a single summary statistic. Demographic rates for the Huai Kha Khaeng plot could not be calculated because of lack of access to data on S, R and DBH (required for calculating basal area).

2.4 | Climate data

We extracted annual temperature and precipitation values for each plot from the 0.0083° by 0.0083° 1951–2000 time-series in the WorldClim dataset (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Using these time-series, we calculated arithmetic mean annual temperature (MAT) and mean annual precipitation (MAP) for each plot.

2.5 | Statistical analyses

Forest inventory analyses from the Americas suggest a threshold-type latitudinal trend of N-fixing tree abundance, with an order of magnitude abundance difference below 35° compared to north of 35° (Menge, Batterman, Liao, et al., 2017; Menge et al., 2014; ter Steege et al., 2006). Rather than explicitly test for such a non-linear response, we divided our data into 'Low' and 'High' latitude categories for analysis. We used 23.44° (Tropic of Cancer) as our latitudinal cutoff to conform to 'tropical' versus 'extratropical', but the exact latitudinal cutoff did not qualitatively influence our results: The American plots were all <10° or >37°, and the Asian plots did not exhibit a latitudinal trend (see Section 3).

To determine how plot-level abundance, taxonomic richness and demographic rates changed across latitude categories and continents, we used a two-way ANOVA (main effects for continent and latitude category, with an interaction between them) with post-hoc differences determined using Tukey's HSD test. To evaluate the relationship between the relative taxonomic richness of N-fixing trees and their relative abundance, we regressed the relative abundance of N-fixing trees against their relative taxonomic richness independently for the different continent (America or Asia) and latitude categories, forcing the regression through zero as in Menge, Batterman, Liao, et al. (2017). To evaluate our question about climate, we regressed the relative abundance of N-fixing trees against MAT, MAP, and their interaction, treating American and Asian plots independently. For the climate analysis, we did not evaluate plots in Europe or Oceania because the number of plots in these regions was too small to compute robust relationships with climate.

2.6 | Dynamic model to infer what patterns of N limitation could explain the abundance of N-fixing trees

The strongest and most interesting pattern we found (see Section 3) was that N-fixing trees were much less abundant in Asian tropical forests than in American tropical forests. One potential driver of this pattern could be a difference in the underlying soil nutrient conditions in the two regions, in particular the degree of intrinsic N limitation. By 'intrinsic N limitation', we mean that a site would be N limited if we could remove the N fixed by tree symbioses. According to theory, N-fixing trees are successful in intrinsically N limited areas, and their N fixation enriches the ecosystem long before the N-fixing trees themselves are competitively excluded (Menge, Batterman, Hedin, et al., 2017). The differential regulation (Menge et al., 2014) and N limitation severity (Menge, Batterman, Hedin, et al., 2017) hypotheses both state that N-fixing trees in the American tropics are abundant because a substantial fraction of American tropical forests is intrinsically N-limited. Following this logic, the low abundance of N-fixing trees in the Asian tropics may be due to a low fraction of Asian tropical forests being intrinsically N-limited.

We could not test this hypothesis, for two reasons. First, we lack the appropriate soil N data at the spatial resolution of our forest plots to establish N limitation, and second, even if such data existed, they would evaluate realised N limitation rather than intrinsic N limitation because N-fixing trees are present. However, although we cannot test the hypothesis, we can use a model to refine the hypothesis. Specifically, we provide a quantitative answer to the question: What fractions of the forested area in the American versus Asian tropics would need to be intrinsically N limited to explain the abundance data we report?

The model we use simulates the successional abundance dynamics of N-fixing and non-fixing trees as they compete for nutrients, in two types of forest habitat: (a) a habitat that is N limited in the absence of N-fixing trees, i.e. a habitat with intrinsic N limitation, and (b) a habitat that is not. The model then calculates the relative abundance of N-fixing trees in each of the two types of habitat, given an age distribution of forests in a region. Appendix S1 provides further details of the model and its application.

All statistical and modelling analyses were conducted in the R programming language (R Development Core Team, 2013). The data used in our analyses are presented in the figures in Appendix S1 and the spreadsheet in Appendix S2, which are part of the Supporting Information (Menge et al., 2019).

3 | RESULTS

In total, we identified 183 N-fixing tree species from 49 genera in our 44 large forest plots (Appendix S3). The majority of these species (169/183, or 92%) and genera (44/49, or 90%) were legumes in the family Fabaceae. However, there were also 14 species (8%) and five genera (10%) that were non-legumes, representing actinorhizal species from five families: Betulaceae, Elaeagnaceae, Myricaceae, Rhamnaceae and Rosaceae. These actinorhizal species occurred in 10 extratropical plots in America (Harvard, Michigan Big Woods, Santa Cruz, SCBI, SERC, UMBC, Utah, Wabikon, Wind River, Yosemite) and two extratropical plots in Asia (Gutianshan, Tiantongshan), except for *Myrica rubra*, which occurred in the two extratropical plots in Asia mentioned and also in two tropical plots in Asia (Fushan, Hong Kong).

N-fixing trees were much less abundant and diverse in the Asian tropics than in the American tropics and Oceania (Q1; Figures 1 and 2, Figures S1–S3; Appendix S2). On average, N-fixing trees comprised 1.5% of basal area and 0.9% of stems in tropical Asian plots, compared with 6.9% of both basal area and stems in tropical American plots. There were no N-fixing trees in the European plots. Relative genus and species richness of N-fixing trees were 3.0% and 2.6% in the Asian tropics, compared with 7.2% and 7.7% in the American tropics. In plots with N-fixing trees, their abundance and diversity were dominated by legume species except in extratropical America, where legume species were often absent and N-fixing abundance and diversity were often dominated by actinorhizal species (Figures S4 and S5). Furthermore, for plots with at least one legume individual, the proportion of legume abundance or diversity due to N-fixers varies widely in the range 0–100%, regardless of the metric used (Figure S6). The trends in abundance and diversity of N-fixing trees remained the same when using absolute instead of relative values (Figures S7–S10), except that the diversity of N-fixing trees in tropical America was generally higher than in other regions (Figures S9 and S10).

In our American plots, relative basal area of N-fixing trees declined 13-fold from low to high latitudes (Q2; Figures 1 and 2). In stark contrast to the Americas, there was no such latitudinal trend in our Asian plots (Figures 1 and 2). Relative genus and species richness of N-fixing trees varied little across latitude within America or Asia (Figure 2, Figures S1–S3).

N-fixing trees had significantly higher mortality than non-fixing trees in extratropical American plots ($p = 0.003$), but not in any other region (Q3; Figures S11 and S12). Neither growth nor recruitment differed significantly between N-fixing and non-fixing trees within or between any of our regions.

Differences in the relative abundance of N-fixing trees between the American and Asian plots were not explained by mean annual temperature or precipitation (Q4), which spanned similar ranges in the two regions (1.6–26.7°C and 625–3,188 mm in America, 4.7–26.9°C and 519–3,761 mm in Asia; Figure 3). Within the regions, N-fixing trees were more abundant in warmer and wetter plots in America ($R^2 = 0.75$, $p < 0.001$), but not in Asia ($R^2 = 0.16$, $p = 0.47$). These different relationships between climate and N-fixing tree abundance in Asia versus America were driven by the tropical plots, and so were not an artefact of having fewer temperate plots in Asia compared to America.

Our dynamic model suggested that the observed abundances of N-fixing trees in the Asian and American tropics are consistent with a situation where ~2%–7% of Asian tropical forests are intrinsically N limited, compared with ~12%–24% in American tropical forests (Figure 4).

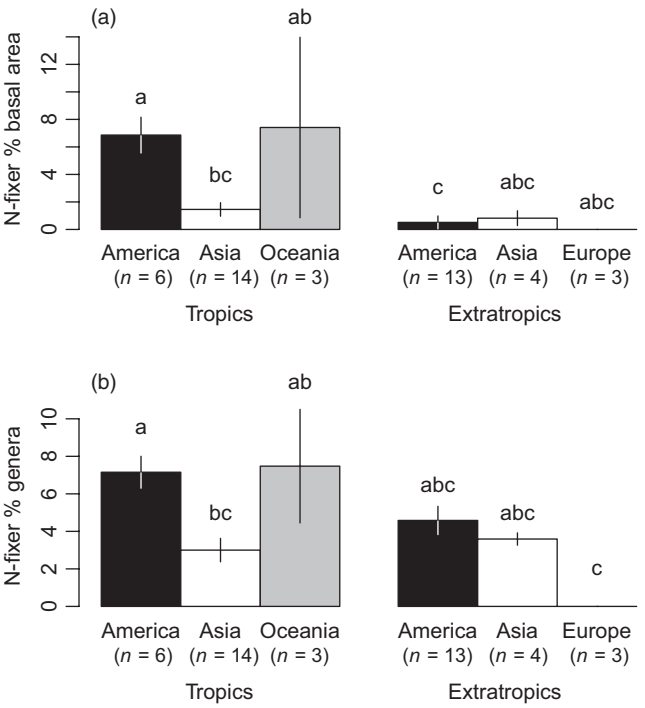

FIGURE 2 Relative basal area (a) and genus richness (b) of N-fixing trees in the CTFS-ForestGEO plots in America, Asia, Oceania and Europe (see Figure 1). Means ± *SE* are shown for each region. The European plots have no N-fixing trees. The extratropical versus tropical divides are the Tropics of Cancer and Capricorn. In total, 44 plots are represented. Plots with the same letter are not significantly different according to Tukey's HSD test

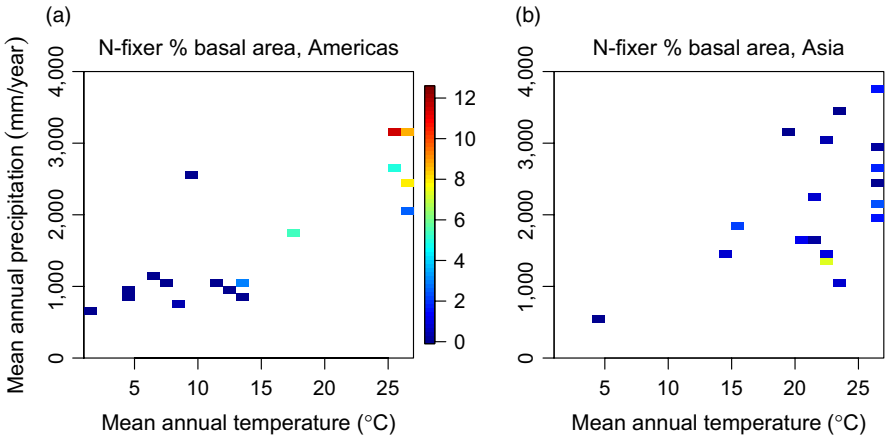

FIGURE 3 Relative basal area of N-fixing trees as a function of mean annual temperature and precipitation in the Americas (a) and Asia (b). There are 19 plots in each panel. Relative basal area is shown in color with the same color scale for each panel. Where a mean annual temperature–mean annual precipitation grid cell encompasses more than one plot, the color is the mean relative N-fixing tree basal area across the plots in the grid cell [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our analyses of 44 large forest plots from the CTFS-ForestGEO network revealed that N-fixing trees were much less abundant in the Asian tropics compared with the American tropics. On average, the proportional number and basal area of N-fixing trees in the Asian tropics were 8 and 5 times lower than in the American tropics respectively. Additionally, the average absolute number and basal area of N-fixing trees per unit area in the Asian tropics were 7 and 5 times lower than in the American tropics respectively. Unlike in America, where N-fixing trees were much more common in the tropics than at higher latitudes, there was no latitudinal trend of N-fixing tree abundance in Asia. Because the disparity in the latitudinal trends between Asia and America was driven by the tropical plots (low abundance in the Asian tropics, high in the American tropics), we focus much of our discussion on the tropical comparison.

The disparity in N-fixing tree abundance between the Asian and American tropics was more extreme than suggested by previous comparisons of legume abundance. In previous studies using smaller sets of CTFS-ForestGEO network plots (Losos & Leigh, 2004; Yahara et al., 2013), legumes in the Asian tropics were 2 times (for the relative number of stems) and 3 times (for relative basal area) lower than in the American tropics (Losos & Leigh, 2004), considerably lower than the 8-fold (for the relative number of stems) and 5-fold (for relative basal area) disparity we found for N-fixing trees. One reason for these differences is that the proportion of legumes that can fix N is lower in the Asian plots (62% and 59% for number of stems and basal area, respectively) compared with the American plots (84% and 74%, respectively).

We also found that N-fixing trees were much less diverse in the Asian tropics compared with the American tropics. On average, the proportional numbers of species and genera that are N-fixing in the Asian tropics were 3 and 2 times lower than in the American tropics respectively. And on average, the absolute numbers of species and genera that are N-fixing in the Asian tropics were 5 and 4 times lower than in the American tropics respectively. These results are

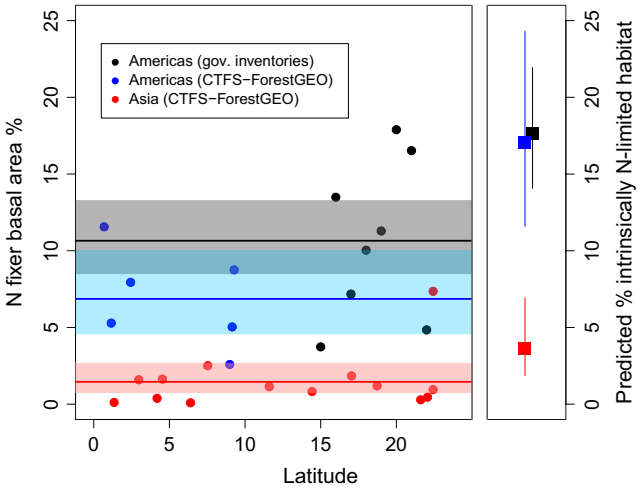

FIGURE 4 The low relative abundance of N-fixing trees in Asia compared with the Americas (left panel) can be explained by a low percentage of intrinsically N-limited habitat (right panel), i.e., habitat that would be N-limited in the absence of N-fixers. The black circles represent means of N-fixer percentage abundance for each 1° latitude from Mexican government inventory data (Menge et al., 2014), whereas the blue and red circles are means for individual CTFS-ForestGEO plots from the Americas and Asia respectively. Each horizontal line and shaded region represent the mean and 95% confidence interval derived by taking the corresponding plot data and fitting a model relating percentage of intrinsically N-limited habitat to percentage of N-fixer abundance. The squares and vertical lines represent the corresponding means and confidence intervals for the percentage of intrinsically N-limited habitat estimated from the model. This model fitted to the two American datasets gave nearly identical mean estimates of the percentage of intrinsically N-limited habitat despite different percentage abundance of N-fixing trees, because the government inventory data encompass the full range of successional ages whereas the CTFS-ForestGEO plots are primarily mature forests [Colour figure can be viewed at wileyonlinelibrary.com]

consistent with those from an early study that used 0.1 ha plots to deduce that the proportional number of species that are legumes in nine Neotropical forest plots was 2–5 times higher than in two tropical forest plots in Southeast Asia (Gentry, 1988).

In this study, we used a dataset that is large in terms of total area and number of trees sampled. However, the forest plots sampled have important differences compared with those used in previous studies of N-fixing tree abundance in the Americas. Here, we used dozens of large plots (mean 25 ha) from the CTFS-ForestGEO network (Anderson-Teixeira et al., 2015), whereas previous studies (Liao et al., 2017; Menge, Batterman, Liao, et al., 2017; Menge et al., 2014; ter Steege et al., 2006) used tens of thousands of small plots (~0.1 ha) from government forest inventories in the USA, Mexico and Amazonia. Both datasets comprise millions of trees, but have different sampling designs. It is therefore comforting that both datasets give similar answers for the latitudinal pattern of N-fixing tree abundance in the Americas. The latitudinal decline in N-fixing tree abundance is 13-fold in the CTFS-ForestGEO plots, similar to the 11-fold decline documented in plots from government forest inventories (Menge, Batterman, Liao, et al., 2017; Menge et al., 2014; ter Steege et al., 2006). The actual abundance differs substantially among the two sets of plots—6.9% of basal area in the Neotropical CTFS-ForestGEO plots were due to N-fixing trees, versus 13% in the Neotropical government inventory plots (Menge, Batterman, Liao, et al., 2017)—but this difference is expected. N-fixing trees are more abundant in dry tropical forests than in their humid counterparts (Gei et al., 2018; Liao et al., 2017; Pellegrini, Staver, Hedin, Charles-Domonique, & Tourgee, 2016). Therefore, rainforests such as those in the Neotropical CTFS-ForestGEO plots are expected to have lower N-fixing tree abundance than forests that span wider aridity gradients, such as those in the government forest inventories.

The climatic differences between Neotropical plots in the CTFS-ForestGEO network and those in the government inventories also help to reconcile another difference between our results and previous findings. Specifically, our result that N-fixing trees in America are more abundant where it is wetter differs from previous findings that N-fixing trees in America and Africa are more abundant in more arid habitats (Gei et al., 2018; Liao et al., 2017; Pellegrini et al., 2016). However, this can be explained by the lack of dry forests (Gei et al., 2018) or savannas (Pellegrini et al., 2016) in the Neotropical CTFS-ForestGEO plots. A previous analysis of Neotropical plots (Liao et al., 2017) found a U-shaped relationship between precipitation and N-fixing tree abundance. Where precipitation was in the range 1,500–3,000 mm/year, which is similar to the precipitation range of most of the CTFS-ForestGEO plots that we considered, N-fixing tree abundance increased in wetter sites, consistent with our result here. The Liao et al. (2017) analysis also found a much steeper relationship below 1,500 mm/year, where N-fixing trees were much more abundant in drier sites.

Our result that N-fixing trees in America are more abundant where it is warmer agrees well with government forest inventories in Mexico and the USA (Liao et al., 2017). Furthermore, our observation that N-fixing and non-fixing trees have similar demographic rates in our mature tropical forests is consistent with previous findings from mature tropical forests in America (Batterman, Hedin, et al., 2013; Menge & Chazdon, 2016). In summary, our findings for America agree with previous analyses of government forest inventories, despite differences in the sampling design of the plots used. Our findings for tropical Asia are based on a greater number of plots than our findings in tropical America, and hence we expect our findings for Asia to be robust to plot sampling design.

The mechanisms driving lower N-fixing tree abundance in the Asian versus American tropics, and therefore the lack of a latitudinal trend in the Asian plots, are much more difficult to establish. Our analyses did not reveal substantial demographic differences between N-fixing and non-fixing trees in the tropical plots in Asia or the Americas, which are in mature forests. Therefore, the low abundance of N-fixing trees in our Asian plots could instead have been driven by demographic drivers that acted earlier in succession, as observed in forests of the USA (Liao & Menge, 2016), or by a low abundance of N-fixing trees at the level of the metacommunity in Asia. The lack of demographic differences may have contributed to the similar size structures of N-fixing and non-fixing trees in the plots (Figure S13). In addition, our analyses rejected mean annual temperature and precipitation, which span similar ranges in our Asian and American plots, as important drivers of the disparity between the continents. However, climate encapsulates myriad nuances beyond annual averages, such as seasonal variation or covariation in temperature and precipitation, which could help to explain the differences in N-fixing tree abundance between the two regions. We focused on mean annual temperature and precipitation because they had been successful in explaining latitudinal variation in N-fixing abundance in the Americas (Liao et al., 2017) and to avoid statistical data-dredging in the absence of theoretical guidance (Anderson, 2008).

Apart from climate, soil nutrients such as nitrogen and phosphorus are thought to be important drivers of N-fixing tree abundance. Unfortunately, we were unable to assess the roles of soil nutrients directly, due to lack of appropriate data. For example, the global soil phosphorus distribution dataset from ORNL-DAAC (Yang & Post, 2011; Yang, Post, Thornton, & Jain, 2013,2014) represents the most complete and comprehensive soil P estimates for locations worldwide, but provides data at a 0.5° by 0.5° resolution, which is four orders of magnitude larger than our forest plots (by area). In addition, metrics that indicate the availability of relevant nutrients are not available for most of our plots. Furthermore, at least for nitrogen, current levels of soil nutrient availability are not the most relevant metric. Rather, the availability of nitrogen in the absence of N-fixing trees—what we call 'intrinsic' N limitation—is more relevant.

Might differences in intrinsic N limitation between the Asian and American tropics explain the lower abundance of N-fixing trees in the Asian tropics? Our model analysis suggests that it could if ~2%–7% of forests in tropical Asia versus ~12%–24% of forests in tropical America are intrinsically N limited, which seems like a reasonable possibility. It is difficult to estimate intrinsic N limitation in any plot, much less across two entire continents, and consequently there is no direct evidence to support this mechanism. Larger rock-derived N inputs in the Asian versus the American tropics (Houlton, Morford, & Dahlgren, 2018) are qualitatively consistent with tropical Asian

forests being less intrinsically N limited, and with tropical Asian soils being generally more fertile (Huston, 2012). However, many other factors are also relevant, such as atmospheric N deposition, N fixation by organisms other than tree symbioses, N mineralization, and the other resources that determine N demand.

Furthermore, given that current patterns of N-fixing tree abundance are a function of past conditions, past values of all the factors determining N supply relative to demand also matter. In this regard, the preponderance of ectomycorrhizal trees that mine organic N (e.g., dipterocarps) (Brearley, 2012; Phillips, Brzostek, & Midgley, 2013) over symbiotic N-fixing trees in Asian tropical rainforests could be seen as indirect evidence of less severe intrinsic N limitation in the past, suggesting that N fixation has not been as strongly selected over evolutionary time as other N acquisition strategies in the Asian tropics. The preponderance of non-fixing legume taxa in Asian tropical rainforests (Sprent, 2009) further supports the idea that N fixation has not been favored over evolutionary time in this region, and simultaneously argues against a biogeographic constraint on the legume family in Asia. Indeed, at the family level (not just N-fixing families) there are broad consistencies in tree species abundances across continents (Etienne & Rosindell, 2012), indicating little biogeographic constraint on trait evolution in general. In addition, the fact that Asian tropical forests store a large amount of carbon compared to American tropical forests (Sullivan et al., 2017) is consistent with the idea that they have historically been more N sufficient.

Regardless of the underlying mechanisms, our findings on the patterns of N-fixing tree abundance have potentially major implications for global biogeochemistry. Global estimates of N fixation are often made by training models to N fixation data from the Americas and extrapolating them to other regions without accounting for differences in the abundance of N-fixers (Houlton et al., 2008; Meyerholt, Zaehle, & Smith, 2016; Ri & Prentice, 2017; Sulman et al., 2019; Wang & Houlton, 2009; Wieder, Cleveland, Lawrence, & Bonan, 2015). In this way, four recent modelling studies estimated that symbiotic N fixation (Meyerholt et al., 2016; Ri & Prentice, 2017; Sulman et al., 2019; Wang & Houlton, 2009) (technically 'newly fixed N'; Ri & Prentice, 2017) in the Asian tropics was 15–30, 30–100, 0–20, or 20–50 kg N ha^{-1} $year^{-1}$ respectively. Our analysis suggests that the upper range of these numbers might be too high, because the paucity of N-fixing trees in the Asian tropics indicates a low capacity for N fixation by trees.

Although our dataset allowed us to make the inferences described above, in particular on differences in N-fixing abundance and diversity between the American and Asian tropics, we caution that our dataset had limited sampling in extratropical Asia and in regions outside America and Asia. Only 4 of our 44 plots (9%) were located in extratropical Asia and this could be augmented in future studies by using more data in this region, for example, from more plots in the CTFS–ForestGEO network or the Chinese Forest Biodiversity Network (CForBio; Feng et al., 2016). In addition, only 3 of our 44 plots (7%) were in Oceania and only 3 were in Europe. Thus, our results for these two regions are tentative, and more samples from a broader range of habitats are required to test their robustness. For example, the absence of N-fixing trees in the 3 European plots arises partly because of lack of sampling in habitats that are most suitable for N-fixing alder species (genus *Alnus*), which are floodplain forests, swamp forests and the shores of lakes and streams (Douda et al., 2014). Furthermore, we were unable to obtain data from any plots in Africa. Legumes are extremely abundant in some areas in Africa (Gentry, 1988; Losos & Leigh, 2004; Yahara et al., 2013), but many of these taxa are unable to fix N (Sprent, 2009), and one study showed that N-fixing trees in dry forests are less abundant in Africa (~10% of basal area) than in South America (~20% of basal area; Pellegrini et al., 2016). Thus, there is a need to integrate forest plots from Africa into future analyses.

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AUTHORS' CONTRIBUTIONS

D.N.L.M., R.A.C. and T.F. conceived the project, analysed data and wrote the paper. All other authors contributed data and edited the paper.

DATA AVAILIBILITY STATEMENT

The tree abundance, demographic and climate data used in this paper are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.t1s010m (Menge et al., 2019) and also from the GitHub Repository: https://github.com/forestgeo/MengeEtAl2019.

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SUPPORTING INFORMATION

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