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RESEARCH ARTICLE

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

Duncan N. L. Menge[1] | Ryan A. Chisholm[2] | Stuart J. Davies[3] | Kamariah Abu Salim[4] | David Allen[5] | Mauricio Alvarez[6] | Norm Bourg[7] | Warren Y. Brockelman[8] | Sarayudh Bunyavejchewin[9] | Nathalie Butt[10] | Min Cao[11] | Wirong Chanthorn[12] | Wei-Chun Chao[13] | Keith Clay[14] | Richard Condit[15] | Susan Cordell[16] | João Batista da Silva[17] | H. S. Dattaraja[18] | Ana Cristina Segalin de Andrade[17] | Alexandre A. de Oliveira[19] | Jan den Ouden[20] | Michael Drescher[21] | Christine Fletcher[22] | Christian P. Giardina[16] | C. V. Savitri Gunatilleke[23] | I. A. U. Nimal Gunatilleke[23] | Billy C. H. Hau[24] | Fangliang He[25] | Robert Howe[26] | Chang-Fu Hsieh[27] | Stephen P. Hubbell[28] | Faith M. Inman-Narahari[16] | Patrick A. Jansen[3,20] | Daniel J. Johnson[29] | Lee Sing Kong[30] | Kamil Král[31] | Chen-Chia Ku[13] | Jiangshan Lai[32] | Andrew J. Larson[33] | Xiankun Li[34] | Yide Li[35] | Luxiang Lin[36] | YiChing Lin[37] | Shirong Liu[38] | Shawn K. Y. Lum[30] | James A. Lutz[39] | Keping Ma[32] | Yadvinder Malhi[40] | Sean McMahon[41] | William McShea[7] | Xiangcheng Mi[32] | Michael Morecroft[40,42] | Jonathan A. Myers[43] | Anuttara Nathalang[8] | Vojtech Novotny[44] | Perry Ong[45] | David A. Orwig[46] | Rebecca Ostertag[47] | Geoffrey Parker[41] | Richard P. Phillips[14] | Kassim Abd. Rahman[22] | Lawren Sack[28] | Weiguo Sang[32] | Guochun Shen[48] | Ankur Shringi[18] | Jessica Shue[41] | Sheng-Hsin Su[49] | Raman Sukumar[18,50] | I-Fang Sun[27] | H. S. Suresh[18] | Sylvester Tan[3] | Sean C. Thomas[51] | Pagi S. Toko[52] | Renato Valencia[53] | Martha I. Vallejo[54] | Alberto Vicentini[55] | Tomáš Vrška[56] | Bin Wang[34] | Xihua Wang[47] | George D. Weiblen[57] | Amy Wolf[58] | Han Xu[35] | Sandra Yap[59] | Li Zhu[32] | Tak Fung[2]

[1]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York; [2]Department of Biological Sciences, National University of Singapore, Singapore; [3]Smithsonian Tropical Research Institute, Forest Global Earth Observatory, Balboa, Republic of Panamá; [4]Faculty of Science, Universiti Brunei Darussalam, Brunei Darussalam; [5]Department of Biology, Middlebury College, Middlebury, Vermont; [6]Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia; [7]Smithsonian Conservation Biology Institute, Front Royal, Virginia; [8]National Center for Genetic Engineering and Biotechnology, Klong Luang, Pathum Thani, Thailand; [9]Department of National Parks, Wildlife and Plant Conservation, Research Office, Bangkok, Thailand; [10]Australian Research Council Centre of Excellence for Environmental Decisions, The University of Queensland, St. Lucia, Queensland, Australia; [11]Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan; [12]Department of Environmental Technology and Management, Faculty of Environment, Kasetsart University, Bangkok, Thailand; [13]Department of Forestry and Natural Resources, National Chiayi University, Chiayi City; [14]Department of Biology, Indiana University, Bloomington, Indiana; [15]Field Museum of Natural History, Chicago, Illinois; [16]Institute of Pacific Islands Forestry, Pacific Southwest Research Station, Hilo, Hawaii; [17]Projeto Dinâmica Biológica de Fragmentos

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.

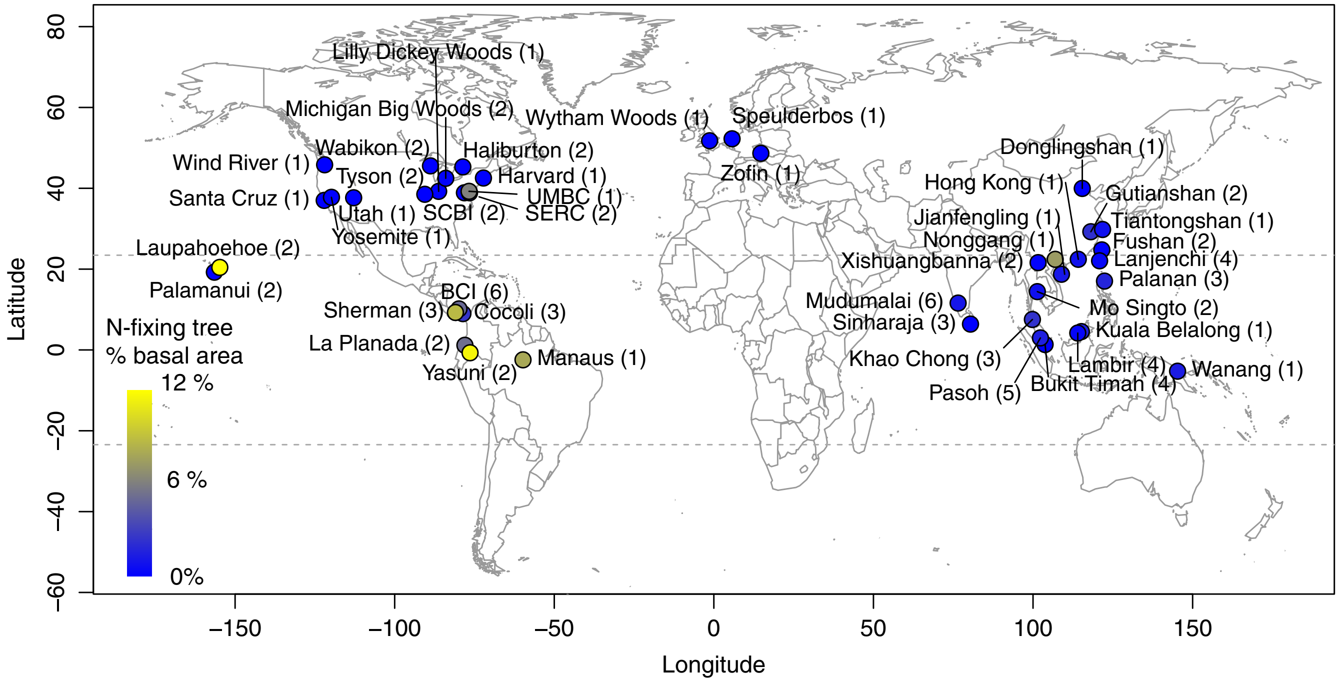

FIGURE 1 Map showing locations and N-fixing tree abundances of the 44 CTFS-ForestGEO plots. Each plot is represented by a circle, together with its name and the number of censuses (in parentheses). UMBC, SCBI, SERC and BCI stand for University of Maryland, Baltimore County; Smithsonian Conservation Biology 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