Received: 1 November 2016 | Revised: 30 January 2017 | Accepted: 2 March 2017

DOI: 10.1111/gcb.13716

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Global climate change will increase the abundance of symbiotic nitrogen-fixing trees in much of North America

Wenying Liao[1,2] | Duncan N. L. Menge[1] | Jeremy W. Lichstein[3] | Gregorio Ángeles-Pérez[4]

[1]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA

[2]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA

[3]Department of Biology, University of Florida, Gainesville, FL, USA

[4]Colegio de Postgraduados, Texcoco, Mexico

Correspondence
Wenying Liao, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA.
Email: wenyingl@princeton.edu

Funding information
National Science Foundation, Grant/Award Number: DEB-1457650

Abstract

Symbiotic nitrogen (N)-fixing trees can drive N and carbon cycling and thus are critical components of future climate projections. Despite detailed understanding of how climate influences N-fixation enzyme activity and physiology, comparatively little is known about how climate influences N-fixing tree abundance. Here, we used forest inventory data from the USA and Mexico (>125,000 plots) along with climate data to address two questions: (1) How does the abundance distribution of N-fixing trees (rhizobial, actinorhizal, and both types together) vary with mean annual temperature (MAT) and precipitation (MAP)? (2) How will changing climate shift the abundance distribution of N-fixing trees? We found that rhizobial N-fixing trees were nearly absent below 15°C MAT, but above 15°C MAT, they increased in abundance as temperature rose. We found no evidence for a hump-shaped response to temperature throughout the range of our data. Rhizobial trees were more abundant in dry than in wet ecosystems. By contrast, actinorhizal trees peaked in abundance at 5–10°C MAT and were least abundant in areas with intermediate precipitation. Next, we used a climate-envelope approach to project how N-fixing tree relative abundance might change in the future. The climate-envelope projection showed that rhizobial N-fixing trees will likely become more abundant in many areas by 2080, particularly in the southern USA and western Mexico, due primarily to rising temperatures. Projections for actinorhizal N-fixing trees were more nuanced due to their nonmonotonic dependence on temperature and precipitation. Overall, the dominant trend is that warming will increase N-fixing tree abundance in much of the USA and Mexico, with large increases up to 40° North latitude. The quantitative link we provide between climate and N-fixing tree abundance can help improve the representation of symbiotic N fixation in Earth System Models.

KEYWORDS
actinorhizal, climate, precipitation, rhizobial, symbiotic nitrogen fixation, temperature

1 | INTRODUCTION

Understanding the extent to which nitrogen (N) availability constrains plants' responses to global climate change is critical for predicting future terrestrial carbon uptake (Hungate, Dukes, Shaw, Luo, & Field, 2003; Stocker et al., 2016). In particular, one of the main challenges of improving Earth System Models is understanding the capacity for biological N fixation to alleviate local N limitation (Stocker et al., 2016). Symbiotic N fixation, particularly the symbiosis between bacteria and angiosperms, has the capacity to overcome N

limitation because it can bring over 100 kg N ha^{-1} $year^{-1}$ into ecosystems (Binkley, Cromack, & Baker, 1994; Binkley & Giardina, 1997; Ruess, McFarland, Trummer, & Rohrs-Richey, 2009) and it can function as a "nitrostat" (Menge & Hedin, 2009), ramping up in response to N limitation. However, this capacity can only be realized when symbiotic N-fixing plants are a sufficiently large part of a local community. In particular, symbiotic N-fixing trees (hereafter "N fixers") can be the dominant source of local N input where they are abundant. Incorporating N-fixation responses and feedbacks into Earth System Models therefore requires an understanding of how the abundance of symbiotic N-fixing trees relates to climate.

How might climate affect the relative abundance of symbiotic N-fixing trees? We look to two types of evidence for developing our expectations: geographic patterns of relative abundance and influences of climate on N-fixation activity. Our geographic evidence comes primarily from forest inventory studies in the Americas. Across a latitudinal gradient, N-fixing trees are abundant (~10% of the basal area) in tropical and subtropical forests but rare (<1%) at higher latitudes (Menge, Lichstein, & Ángeles-Pérez, 2014; ter Steege et al., 2006). Across longitude, N-fixing trees can comprise the majority of the tree community in the southwestern USA, but are essentially absent at the same latitude in the southeastern USA (Menge, DeNoyer, & Lichstein, 2010). Temperature and precipitation both correlate with latitudinal and longitudinal gradients and therefore seem like obvious candidates to help explain patterns of N-fixing tree abundance (Houlton, Wang, Vitousek, & Field, 2008; Jenny, 1950; Pellegrini, Staver, Hedin, Charles-Dominique, & Tourgee, 2016). N-fixing trees' responses to climate may also differ by functional type. Actinorhizal trees (nonlegumes that form symbioses with *Frankia*-type bacteria) are more common in boreal and temperate forests, whereas rhizobial trees (primarily legumes that form symbioses with *Rhizobia*-type bacteria) are more abundant in the tropics and subtropics (Menge et al., 2014), which suggests that different N-fixing functional groups have different temperature responses. However, temperature and precipitation have not been quantitatively linked to N-fixing tree abundance across a tropical-to-temperate gradient, and there are major questions about the shapes of the relationships.

Effects of climate on N-fixation activity likely influence the relative abundance of N-fixing trees, but different lines of evidence suggest different hypotheses about the nature of these influences. Nitrogenases (the enzymes that fix N_2 to NH_3) have unimodal temperature responses, with very low activity below 15°C (Ceuterick, Peeters, Heremans, Smedt, & Olbrechts, 1978; Rainbird, Atkins, & Pate, 1983) and temperature optima ranging from 20°C to 42°C (Ceuterick et al., 1978; Houlton et al., 2008; Prévost, Antoun, & Bordeleau, 1987; Rainbird et al., 1983). At the physiological level, however, arctic N-fixing rhizobia have adapted to lower temperature and maintain function below 0°C (Poinsot et al., 2001; Prévost et al., 1987). Despite this adaptation, physiological measurements also suggest a temperature optimum in a similar range as enzyme activity (Houlton et al., 2008; Rainbird et al., 1983). In contrast to this unimodal relationship, a meta-analysis found that N-fixation fluxes increased linearly with evapotranspiration (Cleveland et al., 1999), suggesting a monotonic (not hump-shaped) temperature response as well as a monotonic precipitation response. N-fixing tree relative abundance depends on the competitive success of N-fixing trees relative to nonfixing trees, which depends on many factors in addition to N-fixation kinetics, physiology, and fluxes. Therefore, a given shape of temperature response (e.g., unimodal or monotonic) for the nitrogenase enzyme does not necessarily translate to a similar temperature response for N-fixing tree relative abundance.

The shape of the relationship between temperature and N fixation has important consequences. A temperature optimum of 25°C for N-fixation activity has been assumed in some studies (Fisher et al., 2010; Wang & Houlton, 2009), which leads to predictions that tropical and subtropical N-fixation fluxes will decline as climate changes (Wang & Houlton, 2009). By contrast, if N-fixing tree abundance increases monotonically with temperature, instead of unimodally, the capacity for N fixation in tropical and subtropical ecosystems would increase in the coming decades, so overall fluxes (which depend on both abundance and activity) could actually increase. Given that N fixation might help drive carbon storage in the globally important tropical forest biomes (Batterman et al., 2013), the shapes of the relationships between climate and N-fixing tree abundance have crucial implications for understanding the carbon-cycle response to climate change.

In addition to temperature, precipitation (or more generally, moisture) is also likely to be an important driver of N-fixing tree relative abundance. The positive relationship between evapotranspiration and N-fixation fluxes (Cleveland et al., 1999) suggests that both temperature and precipitation stimulate N fixation. High precipitation can select for N fixation by (1) increasing N demand, and (2) inducing high N loss via leaching (e.g., Taylor et al., 2015) or gas fluxes (e.g., Houlton, Sigman, & Hedin, 2006), creating a N-limited soil environment (Borken & Matzner, 2009; Tiemeyer & Kahle, 2014). On the other hand, emerging evidence suggests aridity may favor N-fixing trees (Pellegrini et al., 2016). N-fixing trees may have an advantage in arid areas because of (1) low rates of N mineralization and high foraging cost of soil N (Wurzburger & Miniat, 2014), and (2) high water use efficiency related to their high foliar N (Adams, Turnbull, Sprent, & Buchmann, 2016).

Here, we investigate how temperature and precipitation correlate with the relative abundance of symbiotic N-fixing trees within the USA and Mexico, and how future climate change might alter the distribution of symbiotic N-fixing trees, and therefore biogeochemical cycles. We ask: How does the abundance distribution of N-fixing trees (rhizobial and actinorhizal separately, and both types combined) vary with temperature and precipitation? Given the conflicting predictions of enzyme-based versus flux-based studies, and the capacity for adaptation to local temperature regimes, we had competing hypotheses for how temperature would influence N-fixing tree abundance: (1) N-fixing tree abundance increases with temperature (monotonic), or (2) N-fixing tree abundance increases to a peak, then declines at higher temperatures (unimodal). We also had competing hypotheses for the precipitation response. Water use efficiency, N

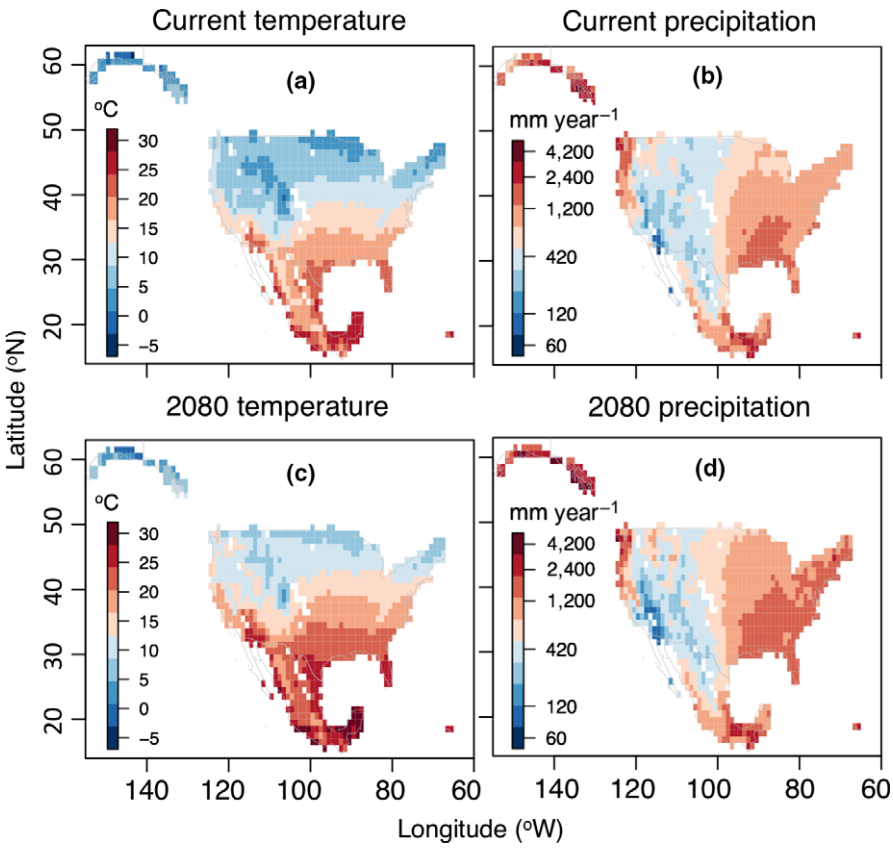

FIGURE 1 Mean annual temperature (MAT) and precipitation (MAP) across Mexico and the USA (the region at top left is southeast Alaska). Current (a, b) and projected (2080; c, d) conditions are shown. Climate data (colors) are only shown in grid cells for which we have forest inventory data. Note that the color scale for precipitation is logarithmic

mineralization, and soil foraging all suggest that (1) N-fixing tree abundance decreases monotonically with precipitation, whereas N loss arguments suggest that N-fixing tree abundance increases in wet environments, leading to (2) a U-shaped response to precipitation. Given the importance of symbiotic N-fixing tree abundance for predicting ecosystem feedbacks to global climate change, we also asked: How will changing climate shift the abundance distribution of N-fixing trees? We used our model fits along with a climate-envelope approach to extrapolate the future distribution of N-fixing trees across the USA and Mexico.

2 | MATERIALS AND METHODS

2.1 | Climate data

We used the Climatic Research Unit (CRU) 10-minute latitude/longitude dataset of mean monthly surface climate, which we retrieved from the British Atmospheric Data Center (BADC) archive (http://www.ceda.ac.uk). The climate elements are calculated based on an archive of monthly average data from more than 4,000 weather stations distributed around the world, covering 1961–1990. We extracted two elements from the dataset: mean annual temperature (MAT, in °C) and mean annual precipitation (MAP, mm/year; Figure 1a,b).

2.2 | Forest inventory data

We used version 5.1 of the USA Forest Service's Forest Inventory and Analysis (FIA) database (http://www.fia.fs.fed.us/) and the Mexican Comisión Nacional's Inventario Forestal y de Suelos (INFyS) database (2004–2007). Plots are systematically distributed in both countries, so they give unbiased estimates of landscape-level patterns. The spatial density is one plot per 2,400 ha forest in the USA, and one plot per 2,500 ha in Mexico. We restricted our analysis to FIA plots measured since 1999 with the national standardized sampling design (Bechtold & Patterson, 2005), which samples trees with a diameter at breast height (dbh) >2.5 cm (four 7.3 m radius subplots per plot, with larger subplots in some western USA regions). The INFyS sampling design is similar but with a minimum dbh of 7.5 cm (four 11.3 m radius subplots per plot). To minimize the effects of different sampling protocols, we restricted our analysis of both FIA and INFyS data to a common minimum dbh of 7.5 cm. We excluded plantations and plots with reported harvest activities.

2.3 | N-fixing tree taxa

Tree species were classified as capable or not capable of N fixation by referencing published reports on nodulation or N-fixation activity (Huss-Danell, 1997; Sprent, 2009). Because N fixation is primarily a genus-level trait (Huss-Danell, 1997; Sprent, 2009), and as many of the species in our dataset have not been evaluated for the capacity to fix N, we classified all species with congeners listed in Sprent (2009) or Huss-Danell (1997) as capable of N fixation, and all other species as incapable of N fixation. In total, we classified 26 genera and 48 species of trees as N-fixing trees in the FIA dataset, and 61 genera and 337 species of trees as N-fixing trees in INFyS dataset.

N-fixing rhizobial and actinorhizal genera are listed for each dataset in Appendix S1.

2.4 | Calculations

Forest Inventory and Analysis and INFyS data were used together to calculate the proportional basal area of N-fixing trees corresponding to each 10′ latitude by 10′ longitude grid cell (as in the CRU climate data). Basal area of each individual tree (BA) is calculated from its dbh as

$$\mathrm{BA} = \pi \times \left(\frac{\mathrm{dbh}}{2}\right)^2.$$

Proportional basal area of N-fixing trees (P_{BA}) at 10′ resolution is the sum of N-fixing tree BA divided by the total BA of all trees in each grid cell.

2.5 | Boosted regression tree analysis

We linked our response variable (P_{BA}) and independent variables (MAT and MAP) using the method of boosted regression tree (BRT) analysis, largely adapted from Elith, Leathwick, and Hastie (2008). BRT is a machine-learning technique that improves the performance of a single model by fitting many models and combining them for prediction. It combines the strengths of two algorithms: (1) regression tree, which uses binary splits to select predictors for the response, and (2) boosting, which combines many simple models to improve predictive performance. Instead of specifying a model before the fit, BRT uses an algorithm to learn the relationship between the response and its predictors (Breiman, 2001). Therefore, it takes into account the interactions among variables automatically and often has improved predictive power. We used this approach because of its flexibility and its ability to handle multicollinear climate data. To implement this analysis, we used the "DISMO" (Hijmans, Phillips, Leathwick, & Elith, 2016) and "GBM" (Ridgeway & Al, 2015) packages in RSTUDIO (R Core Team, 2016).

Partial dependence plots are used to visualize the effect of each climate variable on the response. These plots were generated using partial dependence functions that show the effect of a single variable on the response after integrating out the effect of the other variable in the model; that is, partial dependence plots illustrate the univariate effects of each climate variable (Friedman & Meulman, 2003). Details about generating the graphs are in Appendix S2. In addition, we calculated the observed means and predicted means of P_{BA} for each temperature and precipitation bin, using observed N-fixing tree relative abundance or predicted N-fixing tree relative abundance from boosted regression analysis, respectively.

The relative importance of each predictor variable was measured based on the number of times the variable is selected in the binary splitting, weighted by the squared improvement to the model as a result of each split, averaged over all trees. The results for relative importance and example code for our BRT model are in Appendix S2.

2.6 | Predictions and differences

We compared the predictions generated by BRT with the current distribution of N-fixing trees. Coefficients of determination (R^2; Steel & James, 1960) for the predictions of each fixer category were calculated using the formula:

$$R^2 = \frac{SS_{\mathrm{total}} - SS_{\mathrm{residual}}}{SS_{\mathrm{total}}} = 1 - \frac{\sum (y_i - \tilde{y}_i)^2}{\sum (y_i - \hat{y})^2}$$

where y_i denotes the observed P_{BA}, $\tilde{y}_i$ denotes predicted P_{BA}, and $\hat{y}$ denotes the mean of observed P_{BA}. R^2 represents the proportion of variance explained by our models.

2.7 | Projection of future abundance distribution

Future climate projections were retrieved from the Nature Conservancy website (www.climatewizard.org). Specifically, we used the general circulation model ensemble average, scenario Medium A1B, for MAT and MAP projections in the USA and Mexico. Climate data for year 2080 (Figure 1c,d) and BRT model fits were used to estimate the future abundance distribution of N-fixing trees in each geographic grid cell that is currently represented by FIA or INFyS data. Changes in MAT and MAP are shown in Fig. S1. Like all climate-envelope projections, this relies on extrapolating from a correlation, but the distribution of N-fixing trees in the Americas reflects ecological drivers rather than dispersal or evolutionary limitations (Menge & Crews 2016), and climate is a likely ultimate, if not proximate, driver.

3 | RESULTS

3.1 | All N-fixing trees (rhizobial and actinorhizal combined)

For all N-fixing trees in our dataset, relative N-fixing tree abundance increases with temperature (Figure 2a). Because BRT does not fit a smooth curve to the data, the increase is not strictly monotonic, but after remaining fairly flat below 15°C, relative N-fixing tree abundance rises steadily. We find no evidence for a unimodal temperature relationship. N-fixing trees are predicted to be most abundant at low precipitation, although the decline in abundance might not be monotonic (Figure 2b). As precipitation increases, observations suggest a peak in relative abundance around 2,500 mm/year (Fig. S2b), whereas the model prediction suggests sustained higher abundance above 2,500 mm/year than at 1,200–1,500 mm/year (Figure 2). The discrepancy between observed climate response (Fig. S2) and prediction of univariate climate response (Figure 2) is likely because the predicted univariate response is generated by integrating out the effects of the other variable, whereas observations are mean values in each temperature and precipitation bin, without controlling for variation in the other variable.

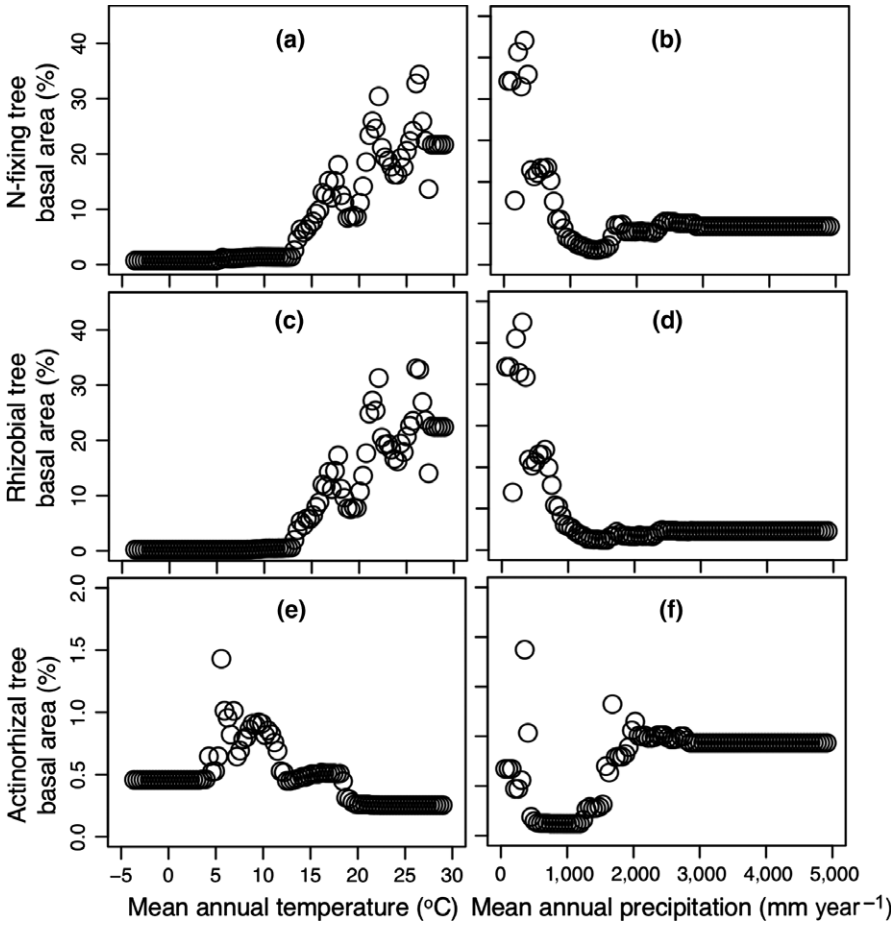

FIGURE 2 Univariate responses of N-fixing tree abundance to mean annual temperature (MAT) and mean annual precipitation (MAP), after integrating out the effect of the other climate variable. Partial dependence plots (from boosted regression tree analysis) are shown as functions of MAT (a, c, e) and MAP (b, d, f), for all N-fixing trees (rhizobial and actinorhizal combined; a, b), rhizobial N-fixing trees (c, d), and actinorhizal N-fixing trees (e, f). Partial dependence plots show the temperature response (a, c, e) after controlling for precipitation effects, and the precipitation response (b, d, f) after controlling for temperature effects. Predicted means that account for variation in both climate variables concurrently (as opposed to a single variable, as shown here) closely match observed means in each climate bin (Fig. S2)

Our BRT prediction explains 46.3% of the variation in N-fixing tree relative abundance (Figure 3a–c). In the majority of the grid cells, predictions match the observations well (Figure 3c). The areas with the highest discrepancies between observations and predictions are concentrated in the southwestern USA (where N-fixing tree are abundant and tend to be underestimated) and northeastern Mexico (where N-fixing tree are less abundant and tend to be overestimated).

We projected the future relative abundance distribution of N-fixing trees based on projected climate conditions in 2080 (Figure 4a, b). Our climate-envelope model suggests that the dominant trend will be an increase in N-fixing tree abundance, driven primarily by warming rather than changing precipitation (Fig. S3a–f).

3.2 | Rhizobial N-fixing trees

Rhizobial N-fixing trees are abundant in Mexico and the southwestern USA, with a pocket of primarily *Robinia pseudoacacia* in the Appalachian Mountains in the eastern USA (Figure 3d). Rhizobial N-fixing trees show similar climatic trends as all N-fixing trees in our dataset (Figure 2c,d). Rhizobial N-fixing trees are most abundant at high temperature and low precipitation. The geographic structure of the residuals (Figure 3f) is also similar for rhizobial and all N-fixing trees in our dataset. The main difference is that rhizobial N-fixing trees are essentially absent from the western half of the USA, north of Arizona and New Mexico, where it is colder (MAT below 15°C) and actinorhizals are the dominant N-fixing trees. Our rhizobial model explains 49.5% of the variance in relative abundance. The projected future distribution of rhizobial N-fixing trees (Figure 4c,d) shows increased relative abundance throughout the southern USA and much of Mexico, which is driven primarily by warming (Fig. S3g–l). These future projections and their primary driver (climate warming) are similar to those for all N-fixing trees (Figure 4a,b).

3.3 | Actinorhizal N-fixing trees

Actinorhizal N-fixing trees reach their highest relative abundance at higher latitudes and altitudes and are concentrated in the Pacific northwest (primarily *Alnus rubra*) and the intermountain west (primarily *Cercocarpus*) in the USA and mountainous areas of Mexico (Figure 3g). Actinorhizal N-fixing trees have different responses to climate variables than rhizobial N-fixing trees. In contrast to rhizobial fixers, the relative abundance of actinorhizal N-fixing trees is predicted to peak around 5–10°C MAT (Figure 2e). Actinorhizal N-fixing trees are rare from ~500 to 1,200 mm/year and increase in relative abundance at both lower and higher precipitation; Fig. S2f). Our model under-predicts actinorhizal N-fixing tree relative abundance near Nevada (Figure 3i), whereas it over-predicts actinorhizal relative abundance in the intermountain west of the USA, concentrated around Montana (Figure 3i). Our model

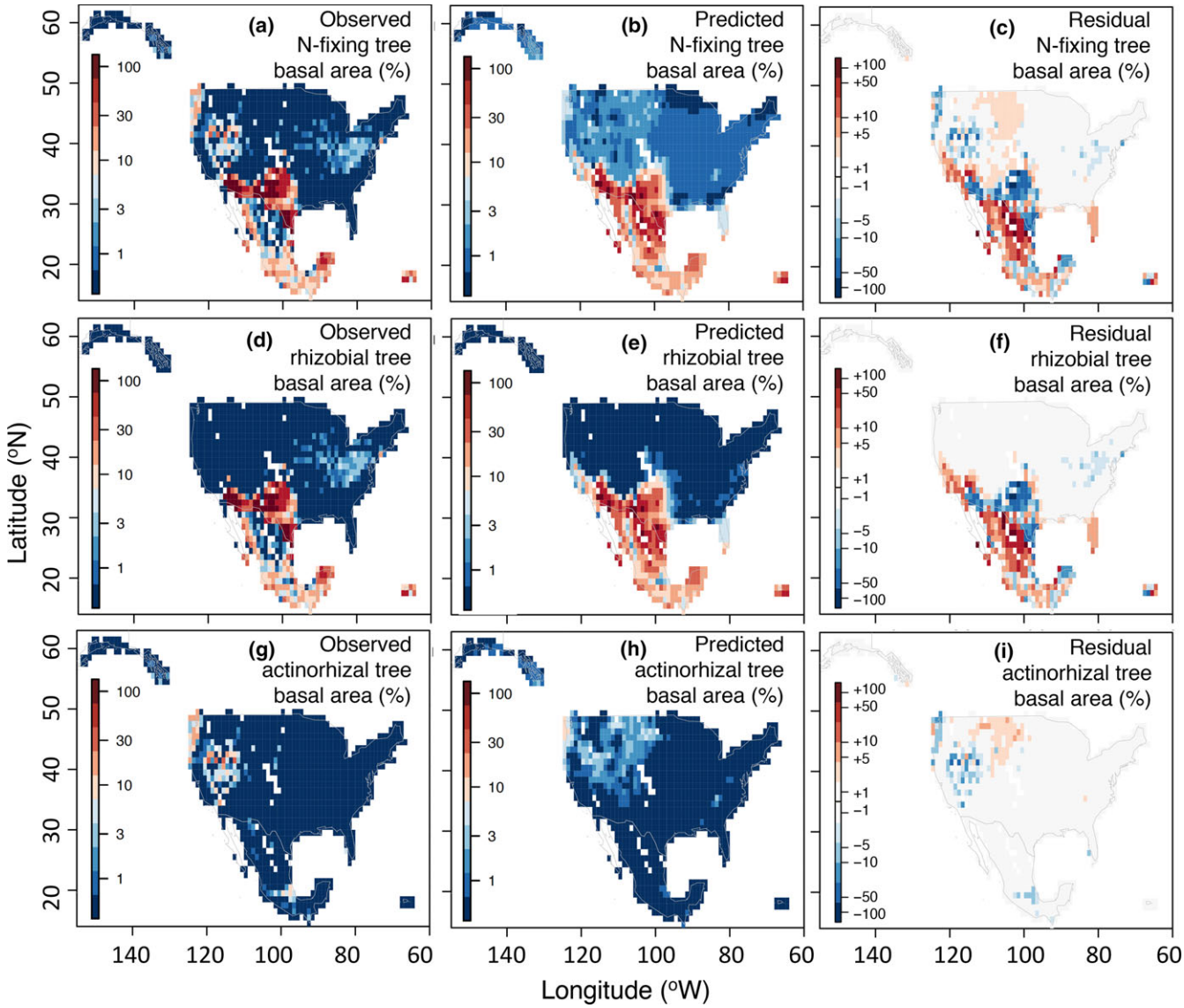

FIGURE 3 Observed and predicted N-fixing tree relative abundance across Mexico and the USA (the region at top left is southeast Alaska). Maps show the observed (a, d, g) and model-predicted (b, e, h) relative abundances, as well as the residuals (prediction–observation, c, f, i), for all N-fixing trees (a–c), rhizobial N-fixing trees (d–f), and actinorhizal N-fixing trees (g–i). Relative basal area is plotted on a log color scale. Our models explain 46.3% (a–c), 49.5% (d–f), and 6.1% (g–i) of variance for N-fixing, rhizobial, and actinorhizal N-fixing tree basal area, respectively

explains only 6.1% of the variation in actinorhizal N-fixing tree abundance (Figure 3g–i). Our climate-envelope model projects that actinorhizal N-fixing trees will become more abundant in southeastern Alaska, where they are currently present but not abundant, and in New England, where tree-sized actinorhizal N-fixing trees are currently rare. These projected increases by 2080 are because of projected warming in southeastern Alaska and projected increases in precipitation in New England (Fig. S3o,r). The climate-envelope projects a decrease in the relative abundance of actinorhizal N-fixing trees in much of the western USA, including the current hotspots of the intermountain west and the Pacific northwest (Figure 4e,f). These decreases are driven largely by increasing temperature beyond the temperature maximum of 5–10°C, along with the relatively dry intermountain west becoming wetter (Fig. S3o,r).

4 | DISCUSSION

According to our model, two commonly used climate variables—mean annual temperature (MAT) and mean annual precipitation (MAP)—explain nearly half of the variation in N-fixing tree abundance across the USA and Mexico. Given the large number of other factors that have been implicated in regulating the abundance of N-fixing trees—for example, nutrients (N, phosphorus, and others), light, herbivory, and successional status (Houlton et al., 2008; Menge, Levin, & Hedin,

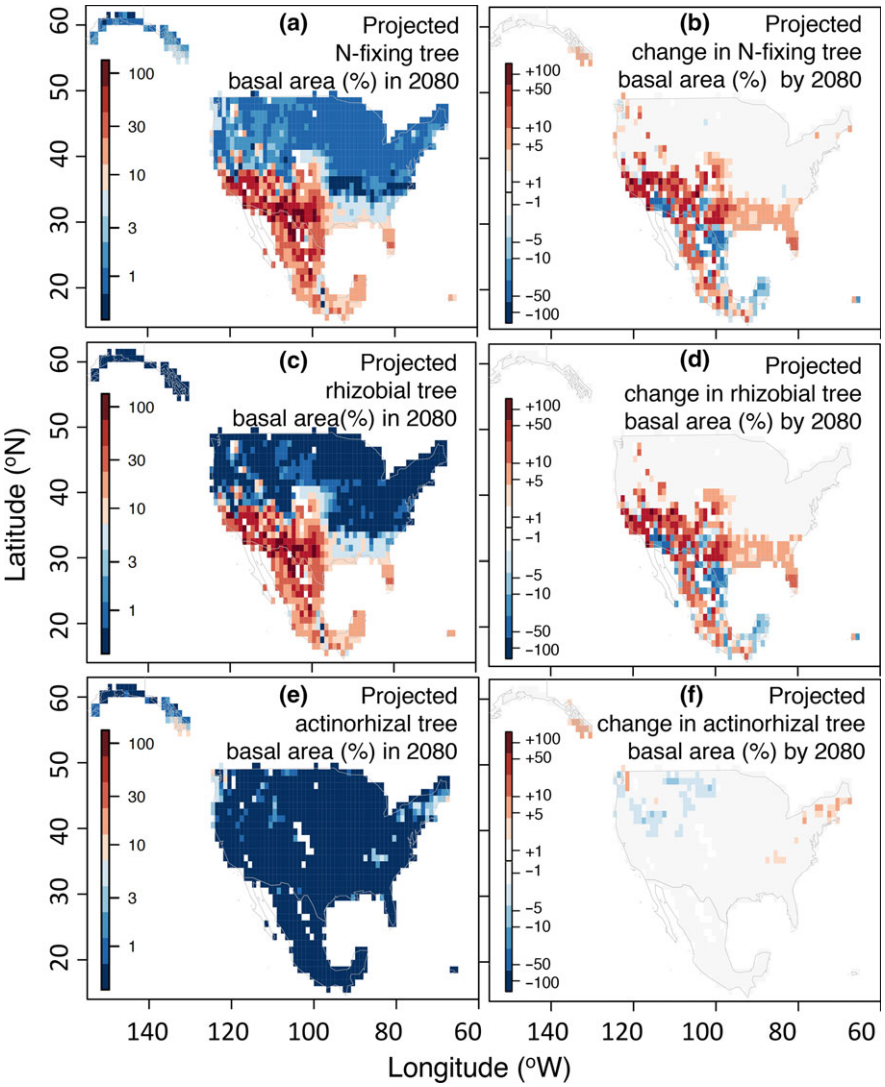

FIGURE 4 Projected future abundance distribution of N-fixing trees across Mexico and the USA (the region at top left is southeast Alaska). The projections are estimated by feeding a climate scenario for 2080 into our model. Projections themselves (a, c, e) and changes from the current predictions to 2080 (b, d, f) are shown for all N-fixing (a, b), rhizobial N-fixing trees (c, d), and actinorhizal N-fixing trees (e, f). Note the logarithmic color scale

2008; Menge et al., 2010; Rastetter et al., 2001; Vitousek & Field, 1999; Vitousek & Howarth, 1991)—it is perhaps surprising that a simple climate-based approach could explain 50% of the variation in N-fixing tree abundance. Although other causal factors may be correlated with climate, the high predictive power of the climate-based approach suggests great potential for improving Earth System Models by incorporating climate constraints on the abundance distributions of N-fixing trees. However, rhizobial and actinorhizal climate responses differed markedly. Rhizobial N-fixing trees are tightly related to climate, whereas actinorhizal trees are only loosely related to climate. Below, we discuss the climate responses of rhizobial and actinorhizal trees, the projected future changes in the abundance distributions of rhizobial versus actinorhizal trees, and the implications of our findings for regional biogeochemical cycling.

4.1 | Rhizobial N-fixing trees are most abundant in hot and dry climates, whereas actinorhizal trees are most abundant in cool climates

As expected from their latitudinal distribution (Menge et al., 2014; ter Steege et al., 2006), rhizobial trees, which are common in tropical and subtropical forests, were abundant in hotter conditions. Conversely, actinorhizal trees, which are rarer overall but relatively common at higher latitudes (Menge et al., 2014), peaked in abundance at lower temperatures. Rhizobial N-fixing trees—and therefore all N-fixing trees in our dataset, of which rhizobial trees comprise 88% of the basal area—are rare when MAT is colder than 15°C and show no sign of decreasing at the warmest MAT in our dataset, 30°C. Therefore, we found no support for the hypothesis that tropical N-fixing tree abundance will decrease as the Earth warms, although our inference is limited to the range of temperatures in our dataset (around −5 to 30°C). It is important to note that an increase in N-fixing tree relative abundance does not necessarily translate into an increase in N-fixation fluxes. N-fixation fluxes themselves depend on both N-fixing tree abundance and the trees' regulation of N fixation, so our results are best interpreted as affecting the capacity for N fixation rather than actual rates. Given the complex links between enzyme activity and community-level N-fixing trees abundance, it is surprising that the temperature response of rhizobial N-fixing tree abundance (low abundance below 15°C) resembles the temperature response of nitrogenase activity (low activity below 15°C, Ceuterick et al., 1978; Rainbird et al., 1983; Prévost et al., 1987). The

alignment of these curves at 15°C is not necessarily the result of a direct causal link; rather, it might be a coincidence, as suggested by the following observations: Sites with a MAT of 15°C are warmer than 15°C for much of the year, particularly in the growing season, so the most relevant temperature for biological activity in these sites is greater than 15°C. Actinorhizal trees in our dataset peak in abundance at 5–10°C, and their symbionts, use the same type of nitrogenase enzyme as rhizobial trees' symbionts (Harriott, Hosted, & Benson, 1995). Evidence from previous studies suggests that actinorhizal trees can fix large amounts of N in places with MAT much lower than 15°C, such as interior Alaska (e.g., Ruess et al., 2009). Finally, herbaceous legumes are relatively common at higher latitudes (Sprent, 2009), suggesting no fundamental limitation on rhizobial activity in regions with MAT <15°C.

At the warmer end of the temperature spectrum, the continuing rise of rhizobial N-fixing tree abundance at 30°C MAT does not support the hypothesis that tropical N-fixing tree abundance will decrease as the Earth warms. Ecosystems with a MAT of 30°C experience temperatures substantially hotter than 30°C, yet rhizobial trees are increasingly successful at least up to a MAT of 30°C. At this warmer end, as opposed to the consistency below 15°C (i.e., low abundance of N-fixing trees and low activity of nitrogenase enzyme), it is harder to relate the abundance and enzyme activity responses to temperature. Although an optimum of 25°C has been used for N fixation in a number of modeling studies (Fisher et al., 2010; Houlton et al., 2008; Wang & Houlton, 2009), different studies show enzyme activity peaks anywhere from 20°C to 42°C (Ceuterick et al., 1978; Prévost et al., 1987; Rainbird et al., 1983) which extends beyond our maximum MAT of 30°C. It is clear, however, that in contrast to rhizobial tree abundance, actinorhizal tree abundance shows little resemblance to the nitrogenase enzyme activity temperature response curve, as the actinorhizal relative abundance peak temperature, 5–10°C, is well below even the lowest reported enzyme activity peak of 20°C.

Rhizobial and actinorhizal N-fixing trees also differed in their relationships with precipitation. As shown recently for tropical savannas and forests (Pellegrini et al., 2016), rhizobial N-fixing trees in the USA and Mexico are most abundant in arid conditions, although they can also be common in mesic and wet conditions. By contrast, actinorhizal trees were as common in wet conditions as they were in dry conditions, with lowest abundance at intermediate precipitation. Theoretically, there are arguments linking N-fixing tree success to both wet and dry conditions (Borken & Matzner, 2009; Wurzburger & Miniat, 2014). In dry conditions, N-fixing trees can maintain their N supply with a lower investment in fine roots near the soil surface (Wurzburger & Miniat, 2014), allowing them to grow deeper roots to access water. Other mechanisms related to high tissue N, such as higher water use efficiency (Adams et al., 2016), might help them survive prolonged periods of drought (Hardwick, 1988). By contrast, the relative advantage of N-fixing trees under wet conditions is likely due to their ability to overcome N limitation caused by leaching.

Why do rhizobial and actinorhizal N-fixing trees differ so markedly in their climate responses? Their evolutionary histories are a good place to start. Rhizobial and actinorhizal trees all reside in the Rosid I clade (Soltis et al., 1995; Werner, Cornwell, Sprent, Kattge, & Kiers, 2014). All confirmed rhizobial N-fixing trees except for *Parasponia* (Akkermans, Abdulkadir, & Trinick, 1978) are in the *Fabaceae* (legume) family (Sprent, 2009), whereas actinorhizal N-fixing trees are spread across eight different families (Huss-Danell, 1997). Both groups have been forming N-fixing symbioses for around 60 million years (Sprent, 2009; Werner et al., 2014). The bacterial symbionts are also phylogenetically distinct. *Rhizobia* are in a different phylum (proteobacteria, which is Gram-negative; Gyaneshwar et al., 2011) than *Frankia* (actinobacteria, which is Gram-positive; Gtari, Ghodhbane-Gtari, Nouioui, Beauchemin, & Tisa, 2012).

Given these differences in evolutionary history, it is not surprising that rhizobial and actinorhizal plants have functional differences in their nodule structure, maintenance of nodule oxygen level, and possibly the way they regulate symbiotic N fixation. Rhizobial plants are better able than actinorhizal plants to regulate nodule oxygen content (Tjepkema, 1988). In fact, the *Frankia* bacteria that colonize actinorhizal plants can maintain low O_2 on their own (Huss-Danell, 1997). Related to these oxygen differences, it has been suggested that actinorhizal trees are ecologically obligate N-fixing trees—fixing the same amount regardless of their N supply and demand—whereas rhizobial trees are facultative N-fixing trees—regulating N fixation to match N supply with demand (Menge & Hedin, 2009; Menge et al., 2014). Higher temperatures might favor a facultative strategy, for at least two reasons. First, regulation of N fixation likely occurs faster at higher temperatures, and faster regulation favors facultative N fixation (Menge, Levin, & Hedin, 2009). Second, mineralization of soil N occurs faster at higher temperatures, so the N supply-demand imbalance might be more dynamic at higher temperatures, selecting for facultative N fixation (Sheffer, Batterman, Levin, & Hedin, 2015).

4.2 | Rhizobial N-fixing trees will become more common with climate warming

Our projections suggest that global climate change will likely increase the abundance of rhizobial N-fixing trees, which could have a significant influence on regional N inputs and C sequestration. Although the largest climate-driven relative abundance increases in North America are in the southwestern USA and western Mexico, the projected increases in the southeastern USA might have the most impact. N-fixing trees are currently relatively common in the southwestern USA and western Mexico, so abundance increases in those regions may not dramatically alter ecosystem function. By contrast, N-fixing trees are currently rare in the southeastern USA, so an incursion of N-fixing trees might fundamentally alter the biogeochemistry of these ecosystems, similar to invasive N-fixing trees in Hawaii (Vitousek, Walker, Whiteaker, Mueller-Dombois, & Matson, 1987). Actinorhizal trees might have similar effects in southeastern Alaska and the northeastern USA, where they are currently rare,

whereas they are projected to decline in abundance throughout much of the intermountain west.

In addition to identifying regional impacts of changes in N-fixing tree distributions, our results provide a clear opportunity to improve Earth System Models. It has become increasingly clear that incorporating the abundance distribution of functional types or traits is pivotal for global climate predictions (Box, 1996; Cox, Betts, Jones, Spall, & Totterdell, 2000; Cramer et al., 2001; Scheiter, Langan, & Higgins, 2013; Verheijen et al., 2015; Woodward & Cramer, 1996; Wullschleger et al., 2014), and our results offer guidance for one of the most important functional groups, N-fixing trees. Despite the limitations of climate-envelope-type approaches —for example, they ignore phenotypic plasticity and genetic adaptation (Charmantier et al., 2008; Chevin, Lande, & Mace, 2010; Hoffmann & Sgro, 2011; Nicotra et al., 2010; Somero, 2010) and how dispersal compares to the velocity of climate change (Loarie et al., 2009)—our results provide a quantitative relationship between commonly measured climate variables and N-fixing tree abundance. This relationship can be used as a constraint in Earth System Models on the capacity for symbiotic N fixation to bring new N into ecosystems.

In the context of improving Earth System Models, our finding that N-fixing tree abundance continues to increase with rising temperature at least up to a MAT of 30°C is particularly important. Assuming a N-fixation activity peak of 25°C suggested a major decline in tropical N-fixation rates as the globe continues to warm (Wang & Houlton, 2009), which would have fundamentally different implications for tropical and global biogeochemistry than continued increases beyond 30°C. Our results do not speak to the process of N fixation per se, but they suggest that the capacity for N fixation—i.e., the abundance of symbiotic N-fixing trees—will remain at least as high as it currently is in the tropics and will increase in much of the subtropics.

5 | CONCLUSIONS AND FUTURE DIRECTIONS

We show that the two functional groups of N-fixing trees (rhizobial and actinorhizal) have different relationships with both temperature and precipitation. N-fixing trees will likely become more abundant in the southern USA and much of Mexico as global climate change continues. Our analysis provides a promising step in predicting future changes in the abundance distribution of N-fixing trees, but important avenues of inquiry remain. For instance, climate is correlated with other potentially causal factors, such as soil type, nutrient status, and land-use history. Future work should attempt to disentangle the causal factors behind the patterns quantified in our study. Despite these remaining questions, our work provides a clear means to improve Earth System Models in the short-term, albeit via a non-mechanistic climate-envelope approach to prescribing N-fixing tree abundance. Predicting and understanding the extent to which N availability will constrain ecosystem feedbacks to future climate change depends on quantifying the capacity for future N fixation (Stocker et al., 2016), which our model provides.

ACKNOWLEDGEMENTS

DNLM acknowledges support from the National Science Foundation (DEB-1457650). Mexico's Comisión Nacional Forestal provided the Mexican forest inventory data.

REFERENCES

Adams, M. A., Turnbull, T. L., Sprent, J. I., & Buchmann, N. (2016). Legumes are different: Leaf nitrogen, photosynthesis, and water use efficiency. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 4098–4103.

Akkermans, A. D. L., Abdulkadir, S., & Trinick, M. J. (1978). N_2-fixing root nodules in Ulmaceae: Parasponia or (and) Trema spp.? *Plant and Soil*, *49*, 711–715.

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

Bechtold, W. A., & Patterson, P. L. (2005). *The enhanced forest inventory and analysis program – National sampling design and estimation procedures*, Vol. 80.

Binkley, D., Cromack, K. Jr, & Baker, D. D. (1994). Nitrogen fixation by red alder: Biology, rates, and controls. In D. E. Hibbs, D. S. DeBell, & R. F. Tarrant (Eds.), *The biology and management of red alder* (pp. 57–72). Corvallis: Oregon State University Press.

Binkley, D., & Giardina, C. (1997). Nitrogen fixation in tropical forest plantations. *ACIAR Monograph Series*, *43*, 297–338.

Borken, W., & Matzner, E. (2009). Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology*, *15*, 808–824.

Box, E. O. (1996). Plant functional types and climate at the global scale. *Journal of Vegetation Science*, *7*, 309–320.

Breiman, L. (2001). Statistical modeling: The two cultures (with comments and a rejoinder by the author). *Statistical Science*, *16*, 199–231.

Ceuterick, F., Peeters, J., Heremans, K., Smedt, H., & Olbrechts, H. (1978). Effect of high pressure, detergents and phaospholipase on the break in the arrhenius plot of azotobacter nitrogenase. *European Journal of Biochemistry*, *87*, 401–407.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, *320*, 800–803.

Chevin, L.-M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology*, *8*, e1000357.

Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Howarth, R. W., Hedin, L. O., . . . Wasson, M. F. (1999). Global patterns of terrestrial biological nitrogen (N_2) fixation in natural ecosystems. *Global Biogeochemical Cycles*, *13*, 623–645.

Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., & Totterdell, I. J. (2000). Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, *408*, 184–187.

Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A., Brovkin, V., . . . Young-Molling, C. (2001). Global response of terrestrial ecosystem structure and function to CO_2 and climate change: Results from six dynamic global vegetation models. *Global Change Biology*, *7*, 357–373.

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*, 802–813.

Fisher, J. B., Sitch, S., Malhi, Y., Fisher, R. A., Huntingford, C., & Tan, S.-Y. (2010). Carbon cost of plant nitrogen acquisition: A mechanistic,

globally applicable model of plant nitrogen uptake, retranslocation, and fixation. *Global Biogeochemical Cycles*, *24*, GB1014.

Friedman, J. H., & Meulman, J. J. (2003). Multiple additive regression trees with application in epidemiology. *Statistics in Medicine*, *22*, 1365–1381.

Gtari, M., Ghodhbane-Gtari, F., Nouioui, I., Beauchemin, N., & Tisa, L. S. (2012). Phylogenetic perspectives of nitrogen-fixing actinobacteria. *Archives of Microbiology*, *194*, 3–11.

Gyaneshwar, P., Hirsch, A. M., Moulin, L., Chen, W.-M., Elliott, G. N., Bontemps, C., ... James, E. K. (2011). Legume-nodulating betaproteobacteria: Diversity, host range, and future prospects. *Molecular Plant-Microbe Interactions*, *24*, 1276–1288.

Hardwick, R. C. (1988). Critical physiological traits in pulse crops. In R. J. Summerfield (Ed.), *World crops: Cool season food legumes* (pp. 885–896). Dordrecht: Springer, Netherlands.

Harriott, O. T., Hosted, T. J., & Benson, D. R. (1995). Sequences of nifX, nifW, nifZ, nifB and two ORF in the Frankia nitrogen fixation gene cluster. *Gene*, *161*, 63–67.

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2016). *dismo: Species distribution modeling*. R package version 1.1-1. https://CRAN.R-project.org/package=dismo

Hoffmann, A. A., & Sgro, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*, 479–485.

Houlton, B. Z., Sigman, D. M., & Hedin, L. O. (2006). Isotopic evidence for large gaseous nitrogen losses from tropical rainforests. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 8745–8750.

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

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

Huss-Danell, K. (1997). Actinorhizal symbioses and their N_2 fixation. *New Phytologist*, *136*, 375–405.

Jenny, H. (1950). Causes of the high nitrogen and organic matter content of certain tropical forest soils. *Soil Science*, *69*, 63–70.

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*, 1052–1055.

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

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

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

Menge, D. N. L., Levin, S. A., & Hedin, L. O. (2008). Evolutionary tradeoffs can select against nitrogen fixation and thereby maintain nitrogen limitation. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 1573–1578.

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

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

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., ... van Kleunen, M. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, *15*, 684–692.

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

Poinsot, V., Bélanger, E., Laberge, S., Yang, G.-P., Antoun, H., Cloutier, J., ... Debellé, F. (2001). Unusual methyl-branched α, β-unsaturated acyl chain substitutions in the Nod factors of an arctic Rhizobium, Mesorhizobium sp. strain N33 (Oxytropis arctobia). *Journal of Bacteriology*, *183*, 3721–3728.

Prévost, D., Antoun, H., & Bordeleau, L. M. (1987). Effects of low temperatures on nitrogenase activity in sainfoin (*Onobrychis viciifolia*) nodulated by arctic rhizobia. *FEMS Microbiology Ecology*, *3*, 205–210.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rainbird, R. M., Atkins, C. A., & Pate, J. S. (1983). Effect of temperature on nitrogenase functioning in cowpea nodules. *Plant Physiology*, *73*, 392–394.

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

Ridgeway, G., & Al, E. (2015). *gbm: Generalized boosted regression models*. R package version 2.1.1. https://CRAN.R-project.org/package=gbm

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

Scheiter, S., Langan, L., & Higgins, S. I. (2013). Next-generation dynamic global vegetation models: Learning from community ecology. *New Phytologist*, *198*, 957–969.

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

Soltis, D. E., Soltis, P. S., Morgan, D. R., Swensen, S. M., Mullin, B. C., Dowd, J. M., & Martin, P. G. (1995). Chloroplast gene sequence data suggest a single origin of the predisposition for symbiotic nitrogen fixation in angiosperms. *Proceedings of the National Academy of Sciences of the United States of America*, *92*, 2647–2651.

Somero, G. N. (2010). The physiology of climate change: How potentials for acclimatization and genetic adaptation will determine winners and losers? *Journal of Experimental Biology*, *213*, 912–920.

Sprent, J. (2009). *Legume nodulation: A global perspective* (pp. 1–181). Oxford, UK: Wiley-Blackwell.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., ... Vásquez, R. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, *443*, 444–447.

Steel, R. G. D., & James, H. (1960). *Principles and procedures of statistics: with special reference to the biological sciences*.

Stocker, B. D., Prentice, I. C., Cornell, S. E., Davies-Barnard, T., Finzi, A. C., Franklin, O., ... Zaehle, S. (2016). Terrestrial nitrogen cycling in Earth system models revisited. *New Phytologist*, *210*, 1165–1168.

Taylor, P. G., Wieder, W. R., Weintraub, S., Cohen, S., Cleveland, C. C., & Townsend, A. R. (2015). Organic forms dominate hydrologic nitrogen export from a lowland tropical watershed. *Ecology*, *96*, 1229–1241.

Tiemeyer, B., & Kahle, P. (2014). Nitrogen and dissolved organic carbon (DOC) losses from an artificially drained grassland on organic soils. *Biogeosciences*, *11*, 4123–4137.

Tjepkema, J. D. (1988). Oxygen regulation and energy usage in actinorhizal symbioses. In N. S. Subba Rao (Ed.), *Biological nitrogen fixation: Recent developments* (pp. 311–339). New York, NY: Gordon and Breach Science Publishers.

Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H. C., Kattge, J., & van Bodegom, P. M. (2015). Inclusion of ecologically based trait variation in plant functional types reduces the projected land carbon sink in an earth system model. *Global Change Biology*, *21*, 3074–3086.

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

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

Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, D., & Matson, P. A. (1987). Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science*, *238*, 802–804.

Wang, Y.-P., & Houlton, B. Z. (2009). Nitrogen constraints on terrestrial carbon uptake: Implications for the global carbon-climate feedback. *Geophysical Research Letters*, *36*, L24403.

Werner, G. D. A., Cornwell, W. K., Sprent, J. I., Kattge, J., & Kiers, E. T. (2014). A single evolutionary innovation drives the deep evolution of symbiotic N_2-fixation in angiosperms. *Nature Communications*, *5*, 1–9.

Woodward, F. I., & Cramer, W. (1996). Plant functional types and climatic change: Introduction. *Journal of Vegetation Science*, *7*, 306–308.

Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., . . . Xu, X. (2014). Plant functional types in Earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany*, *114*, 1–16.

Wurzburger, N., & Miniat, C. F. (2014). Drought enhances symbiotic dinitrogen fixation and competitive ability of a temperate forest tree. *Oecologia*, *174*, 1117–1126.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Liao W, Menge DNL, Lichstein JW, Ángeles-Pérez G. Global climate change will increase the abundance of symbiotic nitrogen-fixing trees in much of North America. *Glob Change Biol*. 2017;23:4777–4787. https://doi.org/10.1111/gcb.13716