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## Biogeochemistry

# Fixing tropical forests

An extensive dataset indicates that nitrogen-fixing trees are most abundant in young, dry tropical forests. The finding expands the potential for natural nitrogen fertilization and carbon dioxide sequestration in areas recovering from land use.

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Tropical forests recovering from deforestation, degradation and agriculture have the potential to remove a significant amount of carbon dioxide from the atmosphere, helping countries meet their climate goals. Recovery of tropical forest is often limited by soil nitrogen availability and can be enhanced by native trees in the legume family that fix nitrogen. But our understanding of the conditions affecting the presence of nitrogen-fixing trees in tropical forests has been biased towards the wet tropics. Writing in Nature Ecology and Evolution, Gei and colleagues[1] provide evidence that, relative to wet tropical forests, legume trees are particularly abundant in dry tropical forests regenerating following recent disturbance. They suggest that high legume abundances in dry tropical forests can be explained by key traits for avoiding nitrogen limitation and heat and water stress.

Understanding the abundance of nitrogen-fixing trees is central to resolving their current and future role in tropical forests. Trees rapidly growing in regenerating tropical forests require large quantities of nitrogen, which is often in limited supply from degraded tropical soils[2]. Nitrogen-fixing trees can supplement insufficient soil nitrogen by unlocking nitrogen directly from the atmosphere with the help of beneficial bacteria. They use this fixed nitrogen to build nitrogen-rich leaf tissue that is eventually made available to neighboring trees during the decomposition of fallen leaves. In theory, a higher abundance of nitrogen-fixing trees means more new nitrogen available to support tree growth, and thus faster forest recovery.

Previous work suggested that nitrogen fixation rates are particularly high in the early stages of tropical forest recovery[3], but whether that translates to higher fixer abundances has only been examined at a few wet tropical forest sites (for example, refs 3-6). Additionally, a handful of studies suggest fixers have an advantage in drier conditions, with higher abundances under aridity in tropical savanna compared to forest biomes[7], greater water use efficiency for trees with higher leaf nitrogen content[8], and ability to either maintain growth during drought or compensate growth following drought through fixation[9,10].

Whether these water-related advantages result in higher fixer abundances in dry tropical forests had not yet been tested using broad-scale analysis. To address these questions, Gei et al. compiled an extensive dataset of forest inventories from 42 chronosequences in recovering wet and dry tropical forests across Central and South

America. The dataset contains basal area of trees from 1,207 0.008-1.3 hectare plots that range in age from 2 to 100 years old and that are grouped by location to make up 42 chronosequences. The authors analysed how the relative abundance of legume trees changes across the chronosequences with successional age and rainfall, and the contribution of trees capable of nitrogen fixation and with bipinnate leaves to changes in legume abundance.

They find that legumes, 93.5% of which they find are nitrogen fixers, are twice as abundant in dry tropical forests than wet tropical forests (Fig. 1). Their analysis indicates this is because dry forest legumes benefit from traits that offer a dual advantage: they can fix nitrogen when the nutrient is scarce; and they have bipinnate leaves that, due to their small size, allow for efficient leaf temperature regulation, less water loss during transpiration and the ability to shed individual leaflets when severely moisture stressed.

Gei and colleagues also find that changes in abundance of nitrogen fixers during tropical forest regeneration differ in dry and wet tropical forest biomes. In wet tropical forests, legumes take up around 18% of the area occupied by trees, regardless of time after forest disturbance (Fig. 1a). But in dry tropical forests, legumes comprise on average 37% of tree-covered area, sometimes reaching 100% in the early phases of recovery, and the abundance of legumes declines as forests recover further (Fig. 1b).

This pattern of abundance for wet forests contrasts with the observed pattern of fixation rates, which start high and decline as forests age[3]. However, the finding is consistent with theory that tropical fixers that use facultative fixation (adjusting fixation rates to their nitrogen balance) would remain present and abundant in the community as tropical wet forests recover, even as nitrogen fixation rates decline to low levels[11].

The findings on dry forests suggest that species in the diverse legume family have more traits than just fixation that help explain their evolutionary success, especially in dry forests. Overall, the authors' results provide the cautionary message that tropical fixers may not all function similarly, whether across recovery ages or tropical forest types.

This study substantially boosts our understanding of the patterns of abundance of nitrogen-fixing trees in tropical forests, but there are several avenues for further exploration. It is not clear why fixers decline in abundance as forests recover in dry but not in wet tropical forest biomes. It will be interesting to explore whether there are fundamental differences in the evolutionary strategies of fixers in the wet versus dry tropics. We also do not now how much nitrogen is actually being fixed in dry tropical forests. With regard to the 83% of variation in fixer abundance that is not resolved by rainfall and forest age, Gei and colleagues show that 45% of this is explained by site (45%), but what differs between sites and what underlies the rest of the variation? Differences in soil nutrients, small-scale forest disturbances like treefalls, seed sources or herbivory levels are all possible contributing factors.

Most fundamentally, Gei and colleagues' study provides the first broad-scale analysis indicating that nitrogen-fixing trees comprise a significant fraction of the tree community during forest regeneration in both wet and dry tropical biomes. Ensuring the protection of diverse nitrogen-fixing species will promote resilience of tropical forests to changes in climate, atmospheric carbon dioxide and human disturbance now and into the future.

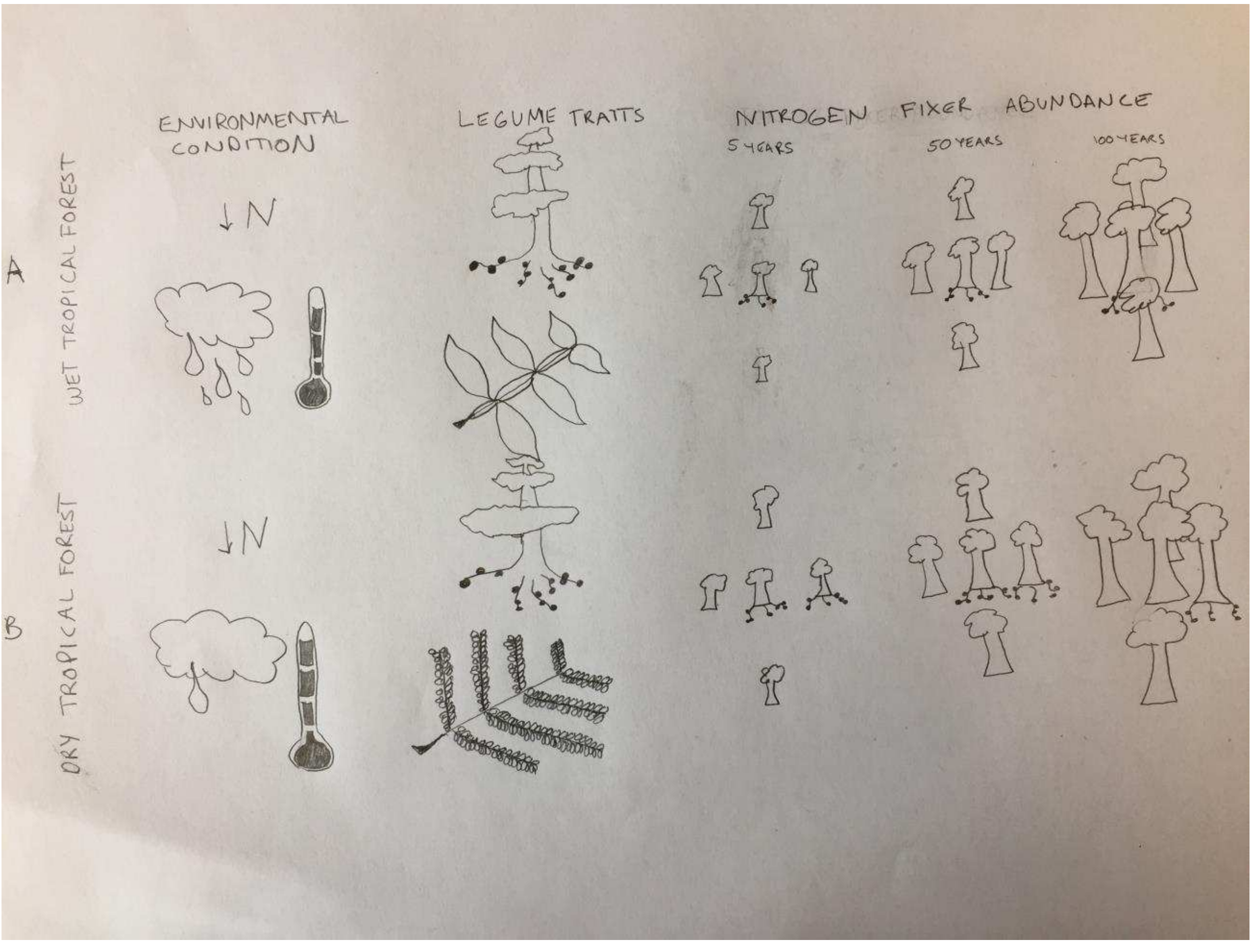


**Figure 1 | Nitrogen-fixing trees in wet and dry tropical forests.** Legume trees in wet tropical forests (**a**) and dry tropical forests (**b**) differ in traits associated with the environmental conditions in which they grow, including the capacity for nitrogen fixation to overcome nitrogen limitation and pinnate vs. bipinnate leaves to avoid stress from heat and drought. Gei et al.[1] show that, in wet tropical forests recovering from disturbance, the proportion of legume trees remains fairly static (on average 18%), regardless of the time after disturbance. However, in dry tropical forests, the proportion of legumes is high in the early phases of recovery (on average 37%) before declining again.

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