

# Functional pathways to building biomass in tropical forests

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Introductions: John Godlee, working on the GEO-TREES project and currently based at the Smithsonian Institution in Washington DC.

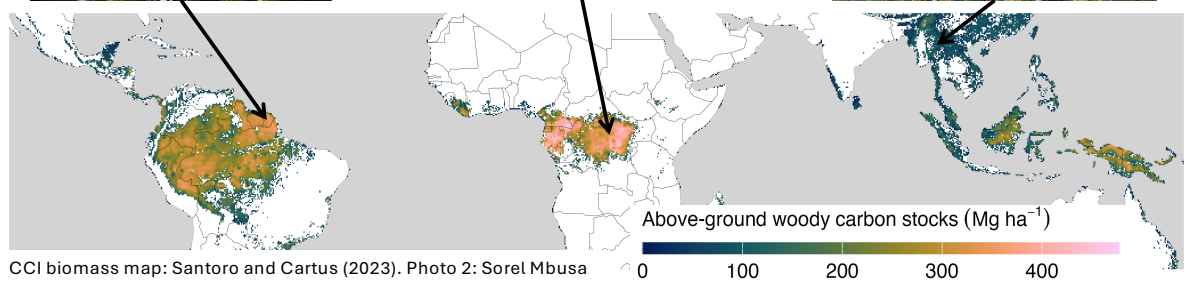
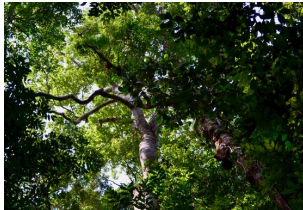
I'm going to talk about the different ways that forests accumulate biomass,  
and how environment and community composition drive those differences.

## Background: The GEO-TREES initiative



Tropical forests are diverse. Variable in structure, function and biomass.

Species determine how environmental conditions translate into biomass and structure.



CCI biomass map: Santoro and Cartus (2023). Photo 2: Sorel Mbusa

Tropical forests are incredibly diverse -- often containing hundreds of species within just a few hectares.

Species differ widely in their life-history strategies, both within a single forest and across regions.

And it's these life history strategies that shape how environmental conditions translate into the biomass stocks we observe.

The environment sets the upper limit for potential biomass stocks, but species traits determine how that potential is realised and expressed through forest structure.

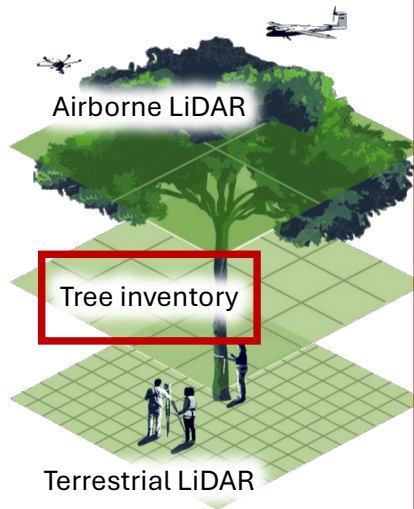
In the GEO-TREES project, we're building a network of forest monitoring sites to facilitate global mapping of woody biomass stocks.

and, along the way this data will also help us to understand the complex interactions between community composition, ecosystem function, and biomass.

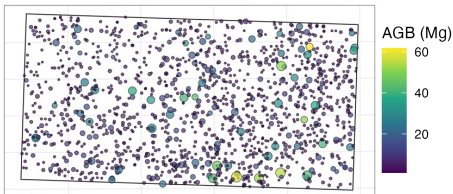
## Background: The GEO-TREES initiative



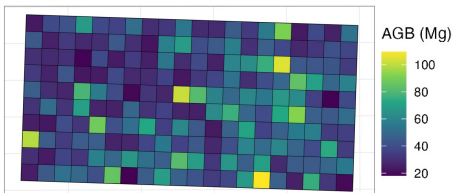
Three data streams:



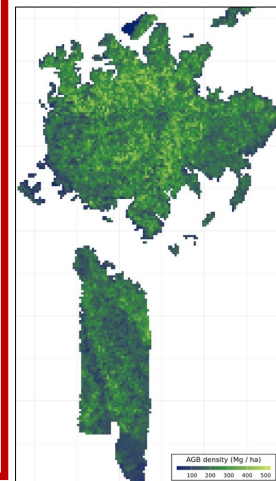
1. Tree-level AGB ( $\geq 5$  cm)



2. 50x50 m quadrat AGB



3. Landscape AGB



The model of GEO-TREES is to map variation in biomass stocks at fine spatial-scales across forest landscapes, using existing sites from many different plot networks that represent the diversity of global tropical forests.

We do this using a combination of tree inventory data, airborne LiDAR and terrestrial LiDAR.

These data can then be used to calibrate and validate biomass estimates from earth observation products across much larger areas.

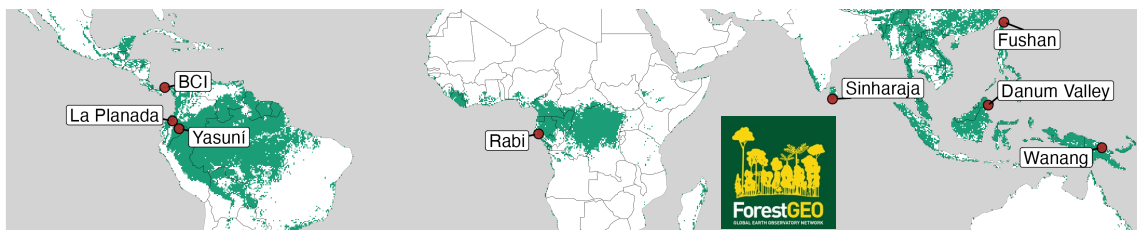
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Today I'll share preliminary results from a study exploring the drivers of this fine-scale spatial variation in woody biomass,

using just the tree inventory data.

## Methods: Sites and data

Do forests follow different “functional recipes” to achieve high biomass?



Community weighted means of species functional traits in 50×50 m quadrats

### Potential growth rate

95<sup>th</sup> percentile basal area growth



### Potential survival

Annual survival of 25% largest trees



### Maximum size

99<sup>th</sup> percentile diameter



### Wood density

Per species  
(Zanne et al. 2009)



In particular, we want to understand how tree community composition and life-history strategies shape spatial patterns in biomass stocks, alongside variation in environment.

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In this study we assembled tree inventory data from wet tropical forests around the world, largely from the ForestGEO network.

We're planning to expand this dataset to include more forest types, so if you have a site with more than 15 ha of tree inventory data, and good soil and topographic data, please come and talk to me afterwards.

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At each site we calculated species-level values of four functional traits, each of which, in isolation, should be positively associated with biomass stocks, increasing either the rate of biomass production, or the biomass residence time.

These traits are:

the potential growth rate, potential survival rate, maximum tree size, and wood density.

We then divided the tree inventory data into 50x50 m quadrats.

At this scale, each quadrat contains enough trees to characterise structure and composition, while still capturing environmental variation across the plots.

For each 50x50 m quadrat, we calculated community-weighted means of these traits, effectively giving us a measure of the functional composition of each quadrat.

We also estimated the total above-ground woody biomass stock using standard allometry methods.

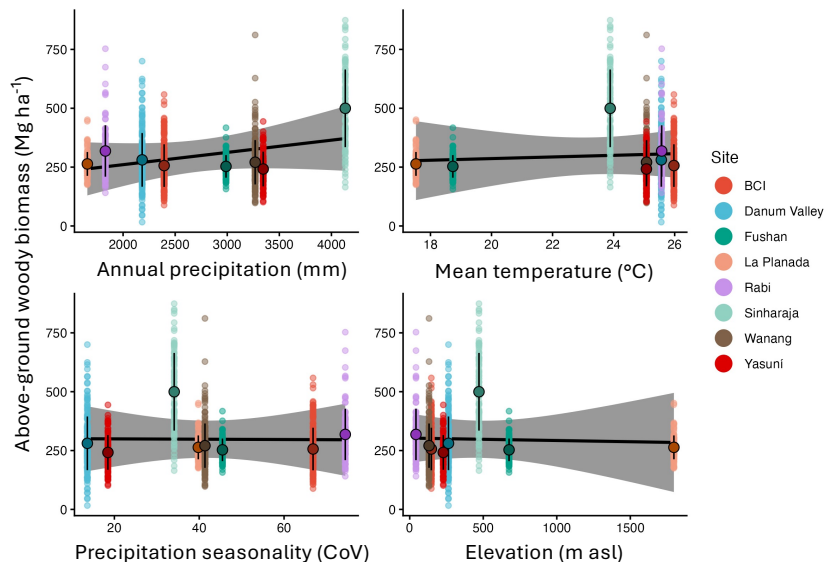
Our expectation is that different forests will optimise different functional pathways to achieve high biomass stocks, depending on biogeography and environmental conditions. In other words, we think that the relative importance of each of these traits for biomass is likely to vary from forest to forest.

## Results: Broad climatic gradients aren't informative

More within- than among-site variation in biomass stocks.

Climate gradient effects on biomass stocks are weak.

Modelling biomass at coarse scales misses fine-scale variation.



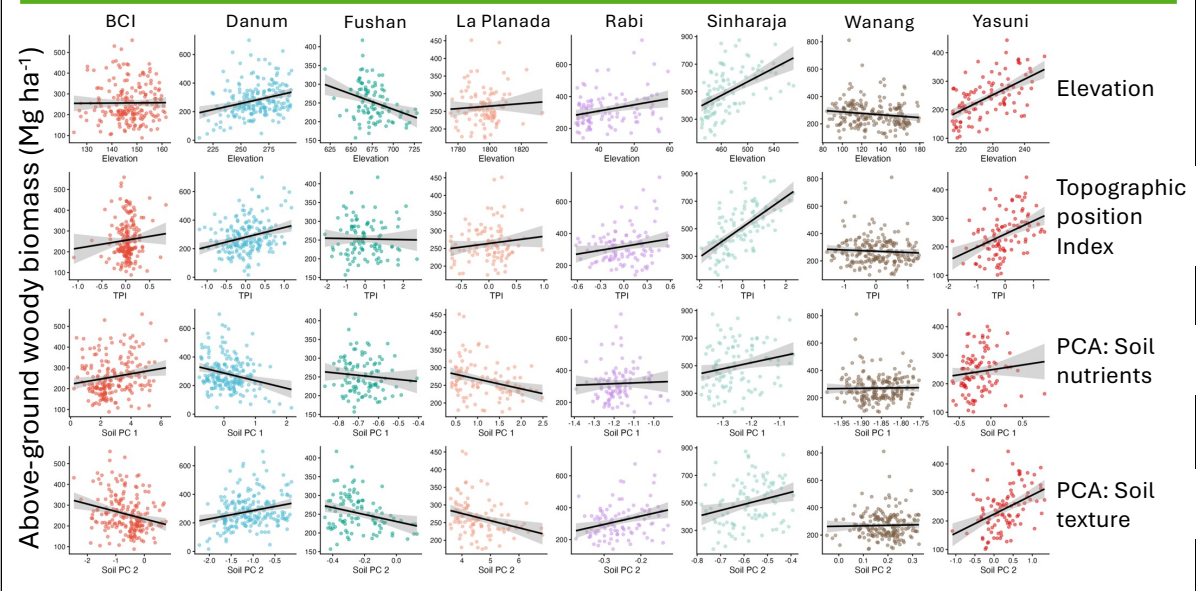
If we start by looking across broad environmental gradients, we find substantial local variation in biomass stocks within sites -- often much greater than the variation among sites.

And across these environmental gradients, there's no strong overall trend in biomass.

This is somewhat surprising because at coarse global scales climate is a strong driver of biomass stocks. Locally however, we see that biomass stocks are extremely variable.

So if we model biomass purely as a top-down, climate-driven process at coarse spatial scales, we risk missing a great deal of this fine-scale variation.

## Results: Site-specific effects of local environment



In contrast, local environmental factors such as soils and topography show much stronger relationships with biomass stocks at this scale.

But, the strength and even the direction of these relationships varies among sites.

This could reflect either: non-linear responses across different parts of a broader environmental gradient, or interactions between local and regional environmental variables.

So, biomass varies at fine spatial scales and this variation is well-explained by local environment, but the form of these relationships varies by site, suggesting that while the underlying processes are deterministic, they are context-dependent.

## Results: Composition is highly predictive of biomass

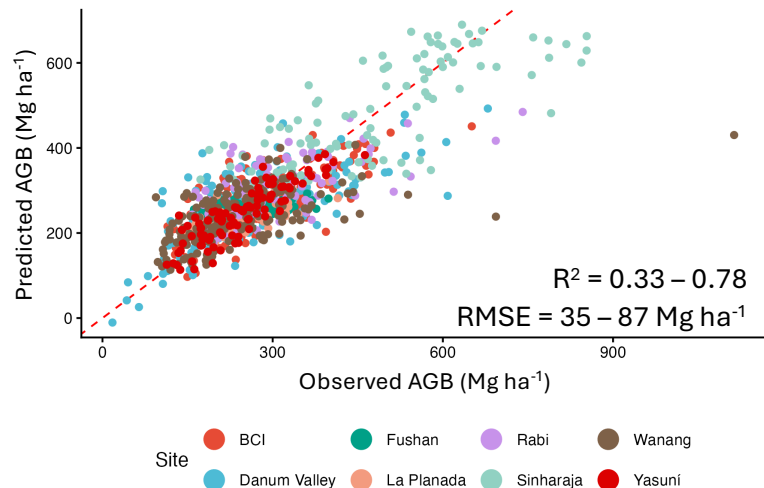
Simple linear models.

One model per site.

Predictors: axes from Principal Coordinates Analysis (PCoA) of composition dissimilarity matrix.

No information on traits or biomass, only relative abundance.

Which aspects of life history strategy drive high biomass?



Next, we asked whether community composition matters for biomass stocks.

We ran a Principal Coordinates Analysis on species relative basal area in each quadrat to produce axes representing compositional variation that are independent of traits and biomass.

When we use these axes to predict biomass stocks within individual sites, we find that composition is strongly predictive.

This tells us that composition does matter, which supports the premise of our question:

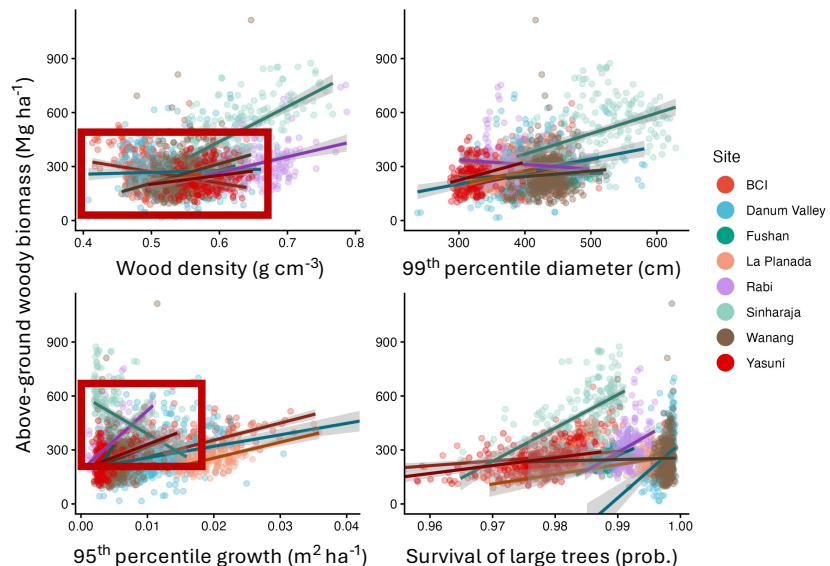
which aspects of life history strategy drive high biomass? What is it about these species?

## Results: Many different recipes for high biomass

Importance of different traits varies by site.

Among sites, similar biomass stocks can result from different trait values.

Negative effects of some traits at some sites implies co-variation of traits.



When we examine how each of our functional traits relates to biomass, we encounter complex patterns.

First, we *do* see clear relationships between traits and biomass within sites, which is reassuring, because it suggests our assumption is correct, that these traits do play a role in driving biomass stocks.

But the slopes of each trait–biomass relationship vary across sites.

Similar biomass stocks can arise from very different trait combinations depending on the site, suggesting different pathways for accumulating biomass in different forests.

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At some sites, certain traits even show *negative* relationships with biomass. All else being equal each trait should increase biomass, so these negative slopes point to strong co-variation among traits and functional trade-offs in community assembly.

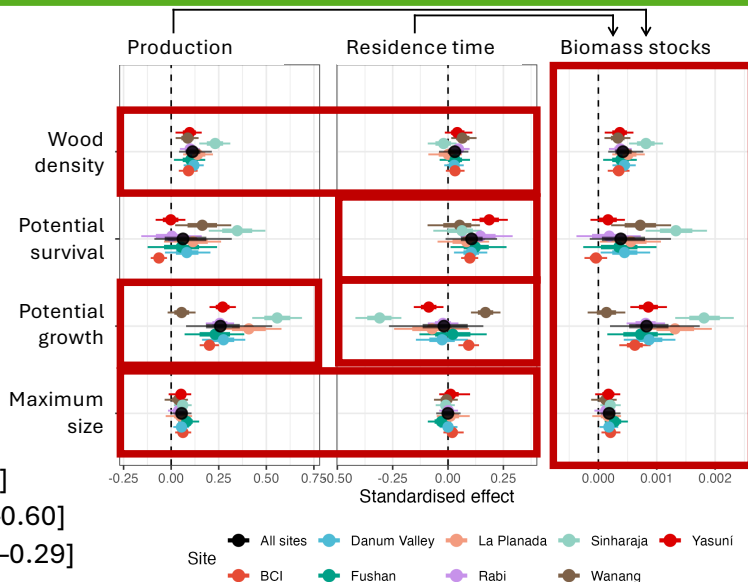
## Results: Importance of community traits for biomass

Importance of growth and survival for biomass stocks varies among sites.

Wood density a consistent driver of high biomass stocks across sites.

Potential size not important. An outcome of growth and survival?

$R^2$  Production: 0.81 [0.79–0.83]  
 $R^2$  Residence time: 0.58 [0.55–0.60]  
 $R^2$  Biomass stocks: 0.25 [0.20–0.29]



To further disentangle how these traits relate to biomass, we built a structural causal model linking our four functional traits to two ecosystem functions: biomass production and biomass residence time, which together determine biomass stocks over the long-term.

We included random slopes for each site so that the effects of traits on production and residence time could vary with environmental context.

Looking at the marginal effects of each trait on ecosystem function, potential growth rate emerges as the strongest overall driver of biomass production, while potential survival is the strongest overall driver of residence time -- exactly as we would expect.

However, there's substantial variation among sites in how important potential growth is for biomass relative to the other traits.

and, interestingly, at some sites, such as Sinharaja in Sri Lanka, higher potential growth rates actually *reduce* biomass residence time, suggesting a community dominated by species with fast-turnover strategies.

Wood density consistently provides a small boost to biomass production across sites, but it has no detectable effect on residence time.

Maximum tree size, on the other hand, has very little influence on either production or residence time.

## Summary: Drivers of fine-scale variation in biomass

- Local environment matters, but differently depending on the forest.
- Community composition is a key predictor of biomass stocks. Forests are not functionally neutral.
- Forests use different “functional recipes” to accumulate biomass. Relative importance of traits varies among sites.
- Functional composition shapes forest structure.



To recap, in this study we examined what drives fine-scale spatial variation in biomass stocks across tropical forests.

We explored the roles of regional and local environment, community composition, and how the importance of specific functional traits for maintaining high biomass stocks varies among forests.

We found that biomass stocks vary enormously within tropical forests at fine spatial scales.

Broad climatic gradients don't explain this variation, but local environment does, though these relationships are site-specific.

We found that community composition is a strong predictor of biomass stocks, showing that forests are not functionally neutral.

We also found that different forests follow different "functional pathways" to accumulate biomass, with traits influencing different aspects of ecosystem function to varying extents depending on site.

## Summary: Perspectives and next steps

- Ground truth data (e.g. GEO-TREES) are vital to understand the mechanisms of biomass accumulation.

Next:

- How do specific environmental factors determine the optimal trait combinations for biomass stocks?
- How does spatial grain affect the importance of community composition for biomass stocks?



Satellite missions such as GEDI, BIOMASS and NISAR, supported by ground-truth data from GEO-TREES, will soon provide wall-to-wall high-resolution biomass estimates. These data are incredibly valuable, but they only tell us how much biomass there is, not the ecology of how it is produced or maintained.

Our results show that if you want to understand how biomass accumulates and how it is likely to respond to perturbations such as climate change and biodiversity loss, you need to incorporate community functional composition and local environment into models of forest dynamics.

The next steps in this analysis will be to understand how specific environmental variables determine the optimal trait combinations to produce high biomass forests,

and to understand how spatial grain affects the relative importance of regional environment, local environment and community composition for observed biomass stocks.

## Thanks and acknowledgements

### Data contributors:

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### ForestGEO analytical workshop – Kenya 2025



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