

A semi-transparent rectangular box is overlaid on the left side of the slide. It contains text in a black, sans-serif font. The background of the slide is a photograph of a forest. The left half of the image is a faded, semi-transparent view of a forest with many trees and green foliage. The right half is a clearer, more vibrant photograph of a forest floor, showing a large tree trunk covered in moss, surrounded by various green plants and ferns.

MEP: ECSC10040

Forest biomass
dynamics

Session 1: 19th October 2022

The carbon cycle,
empirical modelling,
carbon fluxes

John L. Godlee

Today...

1. What is empirical modelling?
2. Background on the carbon cycle
3. Calculating forest growth metrics
4. Constructing a simple model of tree growth/mortality
5. Scaling from individuals to populations

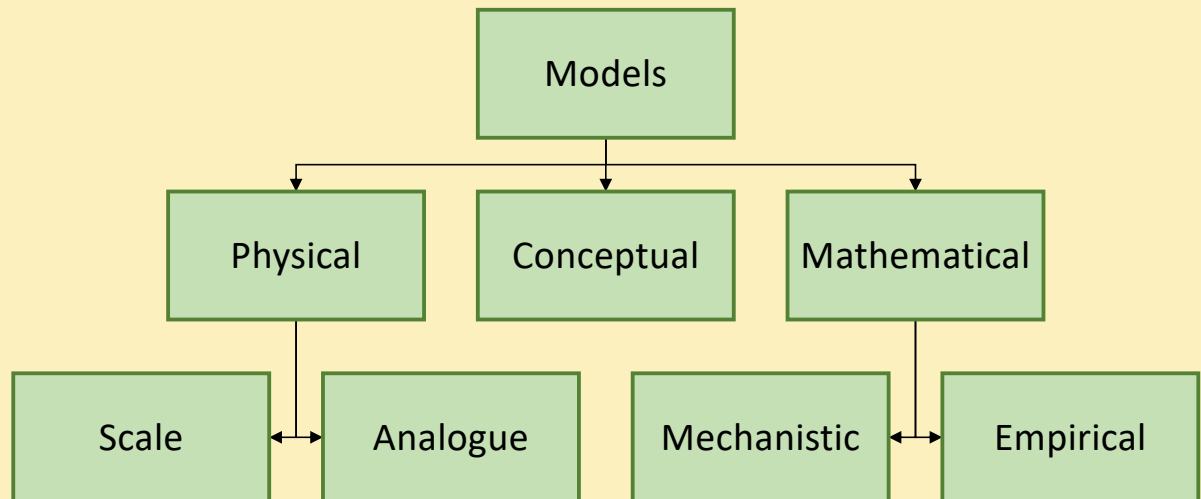
Objectives:

- Understand how population dynamics can be modelled.
- Develop awareness of the factors driving variation in forest biomass dynamics.
- Gain some experience converting maths to R code.



Today we will discuss ...

Empirical vs. Mechanistic modelling



Seen this before in Stace's lectures.

Covered conceptual models.

Physical models are outside the scope of this course really, we don't have the resources.

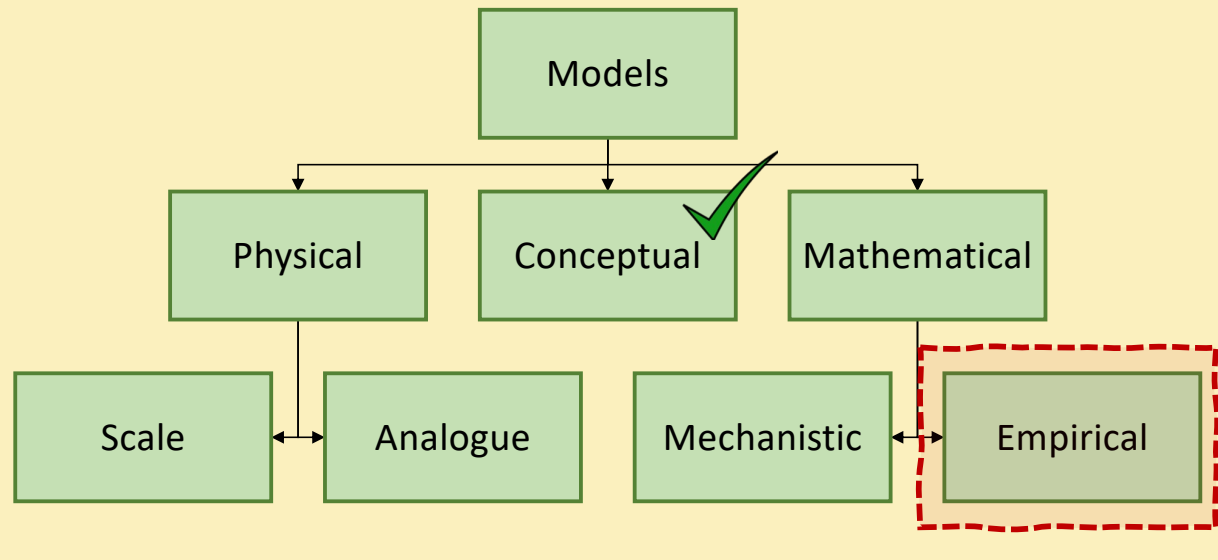
Leaves mathematical models.

We can split mathematical models into mechanistic and empirical models.

In this module we will be focusing largely on empirical models.

In Luke's module, which comes after mine, he will focus mostly on mechanistic models.

Empirical vs. Mechanistic modelling



Empirical vs. Mechanistic modelling

Empirical

- “Top-down”
- Uses observed relationships among data to understand system
- Limited by available data
- Good at:
 - describing an unknown system
 - quantifying observed relationships
- Sometimes:
 - overly simplistic - not realistic
 - wrongly attribute causation

Mechanistic

- “Bottom-up”
- AKA process-based modelling
- Uses rules and assumptions of internal structure to understand system
- Limited by understanding of system
- Good at:
 - making predictions outside observable bounds
 - understanding system behaviour
- Sometimes:
 - impractical to parameterise

Stace covered some of this in his early lectures, but I wanted to recap and add a bit more depth to our distinction of empirical and mechanistic models.

As we shift our thinking to empirical modelling, I thought it would be valuable to define empirical modelling and contrast it to mechanistic modelling.

Although I’m presenting empirical and mechanistic models as two distinct classes of model, in reality it’s a continuum from very mechanistic to very empirical.

Empirical models rely predominantly on using observed relationships among real data to understand a system. This means they are also limited by the availability of that data.

Empirical models don’t make too many assumptions about the underlying structure of the system, all that complexity is expressed through the observed interaction of the variables in the model.

On the other hand, mechanistic models predominantly rely on our understanding of the underlying structure of the system to describe the overall behaviour of the

system.

Because empirical models don't make many assumptions about the system, they are very appropriate for describing a system which we don't know much about.

On the other hand, mechanistic models are better for understanding more deeply the behaviour of a system. Mechanistic models are also good at making predictions outside the observable bounds of the system. If we make some basic assumptions about how the system works, we can do experiments where we tweak the parameters of the model to see how the system would behave under conditions that we haven't been able to observe in real life.

Because of the way empirical and mechanistic models differ in their approach to describing a system, we can also refer to these models as either "top-down" or "bottom-up". I.e. mechanistic models start small, maybe our understanding of how photosynthesis works at the cellular level, and build up to describing the productivity of a whole forest. Empirical models start big, with the relationships we observe in real life.

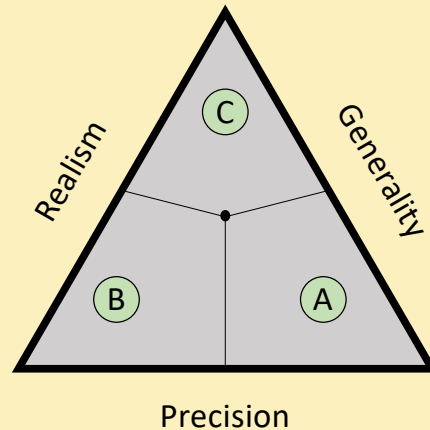
Empirical models are sometimes criticized for being overly simplistic, and because of their high level approach sometimes they are accused of wrongly attributing causation.

Similarly, mechanistic models have their drawbacks. They are highly limited by our understanding of the system. Additionally, mechanistic models can sometimes be very creaky, they are hard to parameterise, and because of their complexity, can break if pushed outside their boundaries.

Generality - Precision - Reality

- A. General and Precise
 - e.g. statistical models
 - Good for: describing systems
- B. Precise and Realistic
 - e.g. mechanistic models
 - Good for: understanding system behaviour
- C. Realistic and General
 - e.g. conceptual models
 - Good for: theory development

Must also consider tractability -
can we parameterize the model?



Levins et al. (1966)

Another way to think about this variation in model type comes from Richard Levins, who described models as a trade-off between Generality, Precision, and Realism. His philosophy was that any model could maximise two of the three parameters, but not all three. A model which was perfectly precise, generalizable to every situation, and totally realistic in its mechanics would not be a model anymore, it would be an identical copy of reality.

So let's think about different models which maximise two of the parameters.

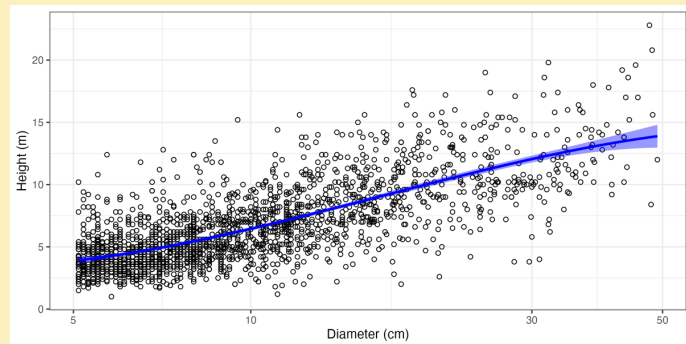
By the way, all the references at the bottom of the slides are included in the lecture slides at the end, so you can read further on the subject.

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Linear regression of tree diameter vs. height



Feldpausch et al. (2011)

A statistical model like a linear regression can be very general while also being very precise. With a statistical model we know what our uncertainty on any arbitrary estimate is. They are good at describing a system, but rely on having data to work with. But statistical models are not particularly realistic. In this example, there appears to be a fairly tight correlation between the diameter and height of trees. But, from this model we get little clue as to what the underlying mechanism is. Due to the limitations of the data, we also have fairly hard limits on the maximum diameter from which we can reliably estimate height.

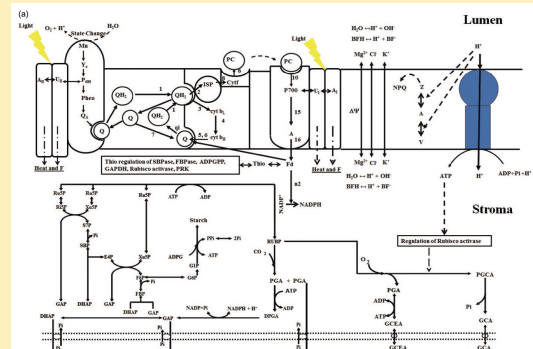
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Zhu et al. (2013)

Photosynthesis at the cell level



$$V_{M1} = \frac{V_{M1max} \left(\frac{[ADP][Pi]}{K_{mADP}K_{mPi}} - \frac{[ATP]}{K_{mATP}} \right)}{\left(K_{mADP}K_{mPi} \right) \left(1 + \frac{[ADP]}{K_{mADP}} + \frac{[Pi]}{K_{mPi}} + \frac{[ATP]}{K_{mATP}} + \frac{[ADP][Pi]}{K_{mADP}K_{mPi}} \right)} \quad (17)$$

$$kE = e^{(-\Delta G/RT)} \quad (18)$$

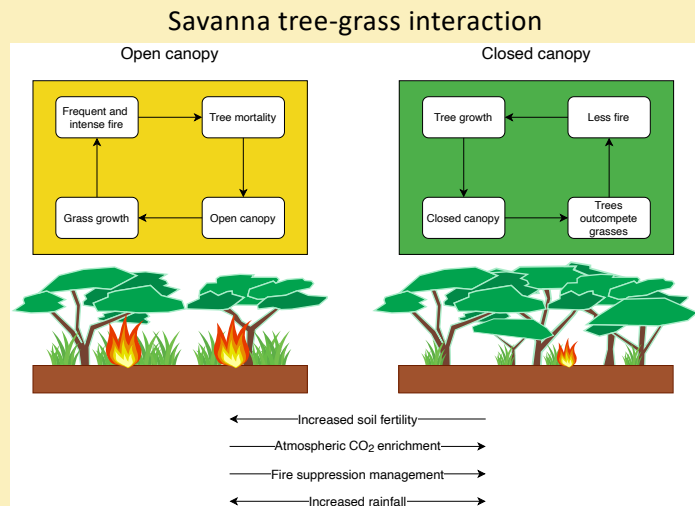
$$\Delta G = \Delta G^{\circ} + 0.592 \text{ HPR} \ln \left(\frac{[H_2]}{[H_2^+]} \right) + \text{HPR} \Delta \Psi \quad (19)$$

A highly mechanistic model is both precise and realistic. This model of photosynthesis at the cell level, which is far too complicated for me to fully understand, uses known rates of chemical diffusion and light use efficiency to predict the production of ATP. This model is not very general however. It describes one thing very well, but cannot model photosynthesis of a CAM plant for example, which uses a different photosynthetic pathway.

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Must also consider tractability -
can we parameterize the model?



Staver et al., (2011)

Conceptual models can be very realistic and highly general. They are not constrained by data availability or deep understanding of the basic mechanics of the system. However, they are not very precise at all. Conceptual models don't use numeric values, often only as much as directional increase or decrease of a given variable.

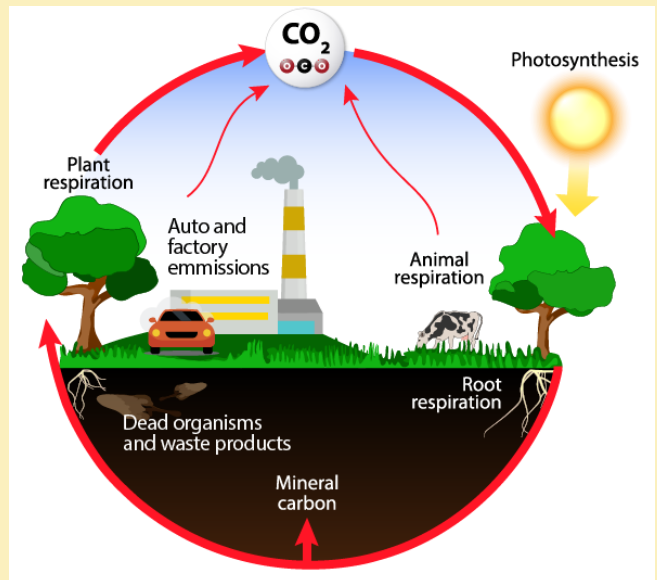
Going back to the PGR triangle, it would be possible to have a model which sits squarely in the middle of the three trade-offs, being equally general, precise, and realistic, but then we have to think about the model tractability. There's no point in designing a model that you then can't parameterise.

Ultimately different models are useful for different things, and as long as you remember that, there's no need to think of any model type being inherently better or worse than another.

The carbon cycle

The simple version (conceptual model):

- CO₂ flux to atmosphere via respiration, combustion
- CO₂ flux from atmosphere via photosynthesis
C stored in biomass, soil, deep geological stores



Now we move onto some background on the content I'm going to teach today.

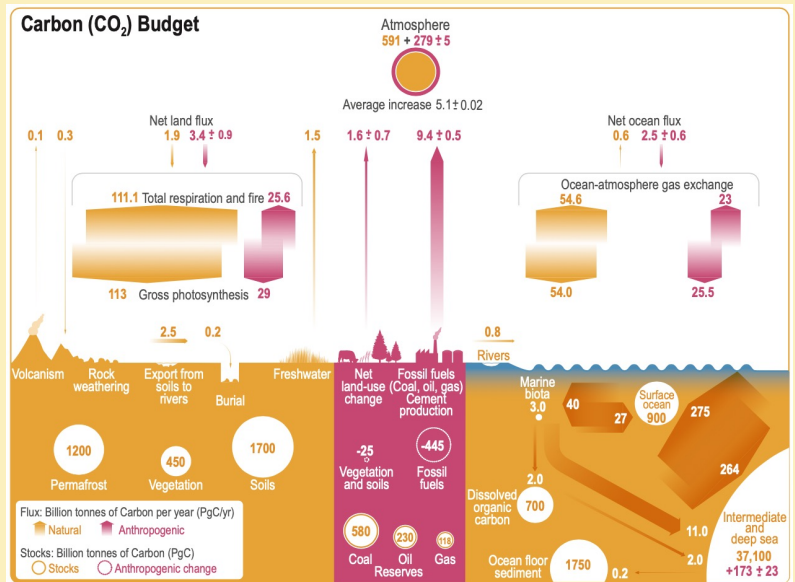
Carbon cycle

The simple version

The carbon cycle

The more complex version (empirical/mechanistic):

- Many sources and sinks, with numeric estimates of magnitude and uncertainty.
- Ability to forecast by changing parameters.
- Interactions among state variables.

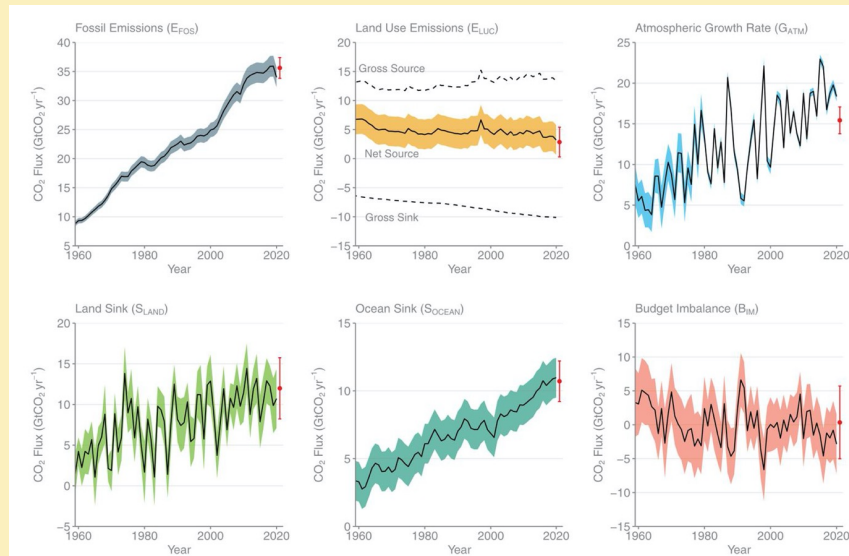


Canadell et al. (2021)

The complex version

Balancing the carbon budget

- Fossil fuel emissions continue to rise.
- The biosphere appears to be responding.
- Increase in terrestrial and oceanic carbon sink.
- But lots of variation and uncertainty on estimates.



Friedlingstein et al. (2021)

Plots from the global carbon budget.

Modelled estimates of carbon emitted or sequestered by different pools.

Fossil fuel emissions are rising

Ocean sink is clearly increasing.

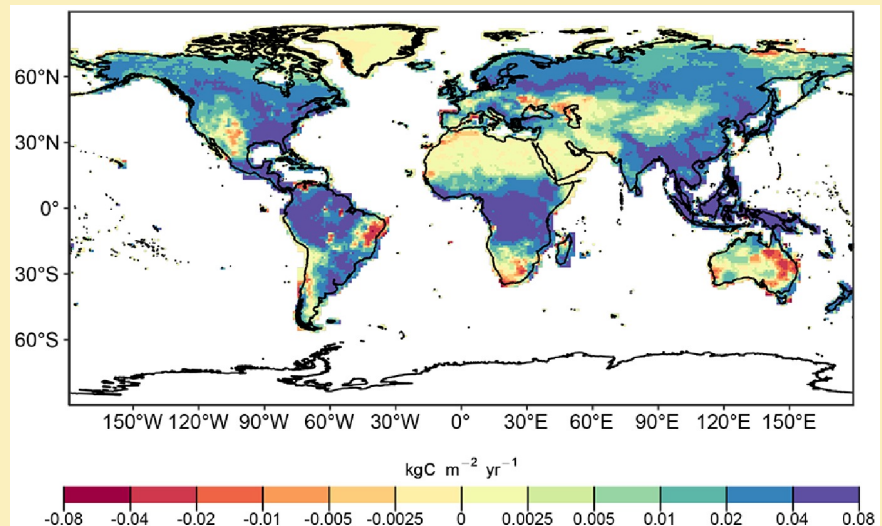
Land sink appears to be increasing, but there's lots of uncertainty in the estimates of the sink, and lots of inter-annual variability.

The terrestrial carbon sink

Most terrestrial ecosystems appear to be sequestering more carbon than they emit.

But these coarse models need to be ground-truthed.

How can we use empirical modelling to measure the forest carbon sink?



Sitch et al. (2015)

This map comes from another mechanistic model, which shows that most terrestrial ecosystems appear to be sequestering more CO_2 than they release (blue areas). Some hotspots of high emission (red areas).

Not a satellite image, a modelled estimate.

The model behind this map uses assumptions about the behaviour of terrestrial ecosystems combined with observations to predict their response to climate and land-use change.

These models need to be parameterized to provide realistic estimates of the terrestrial carbon flux.

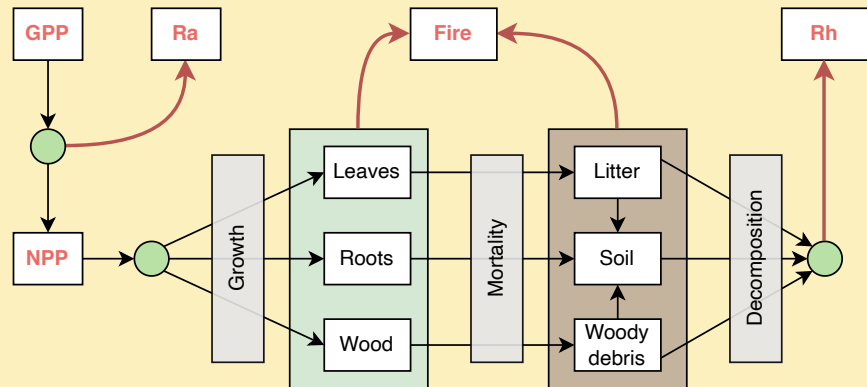
We can use empirical modelling techniques to describe the complex behaviour of ecosystems using observed data.

Zooming in: forest carbon fluxes

- GPP = Gross Primary Production
- NPP = Net Primary Production
- Ra = Autotrophic respiration
- Rh = Heterotrophic respiration

We can measure **growth, mortality, and recruitment** of juveniles in the field to track population dynamics.

We can use these measurements to build models of forest carbon dynamics and estimate the terrestrial carbon sink.



Bloom et al. (2016)

Zooming in a bit further, we can create a conceptual model of internal carbon fluxes in a forested ecosystem.

GPP is the rate of atmospheric carbon uptake by the ecosystem, i.e. how much CO₂ is fixed during photosynthesis.

Some of this is then returned to the atmosphere via autotrophic respiration, and some is fixed into biomass, whether that is leaves, wood, or roots.

These components can die, and be sent to other carbon pools in the system where they eventually decompose and are returned to the atmosphere via heterotrophic respiration, or they can be combusted by fire and sent back to the atmosphere that way.

Luke will go into much further detail on parameterizing this conceptual model in his sessions.

Just know that this is a model, it doesn't perfectly represent reality. In reality, for example, not all NPP is fixed into biomass, some is fixed in sugars and non-structural

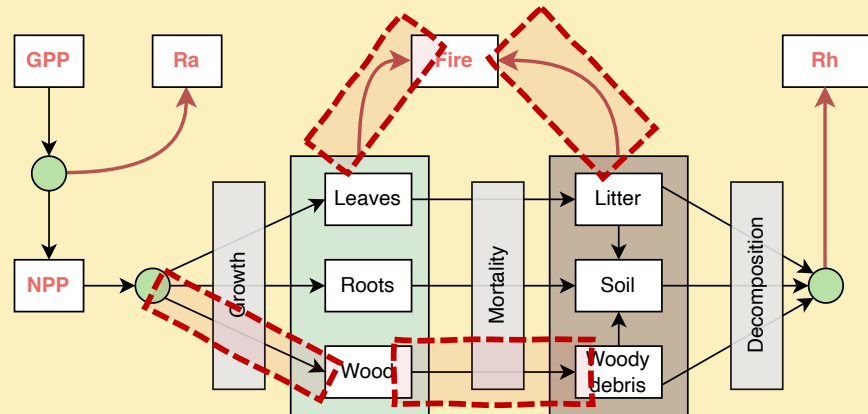
carbohydrates that act as energy stores.

Zooming in: forest carbon fluxes

- GPP = Gross Primary Production
- NPP = Net Primary Production
- Ra = Autotrophic respiration
- Rh = Heterotrophic respiration

We can measure **growth, mortality, and recruitment** of trees in the field to track population dynamics.

We can use these measurements to build models of forest carbon dynamics and estimate the terrestrial carbon sink.



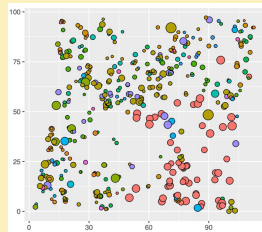
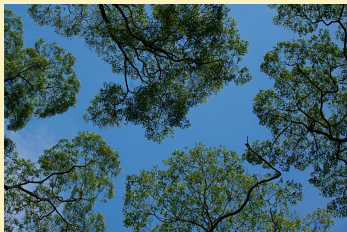
Using data from forest trees, we can parameterise this model by measuring the growth of the woody component of the living carbon pool and the flux of wood from the living pool to the dead pool.

With sufficient data, we can also partition the **decomposition** and **fire** fluxes to the atmosphere.

In addition, using forest tree data, we can partition the growth flux into the recruitment of new trees into the system, and the growth of existing trees.

Field observations

- Tree species
- Stem diameter
- Tree height
- Mortality events
- Wood density
- Canopy architecture
- Number of stems
- Spatial distribution
- Recruitment (seedlings)



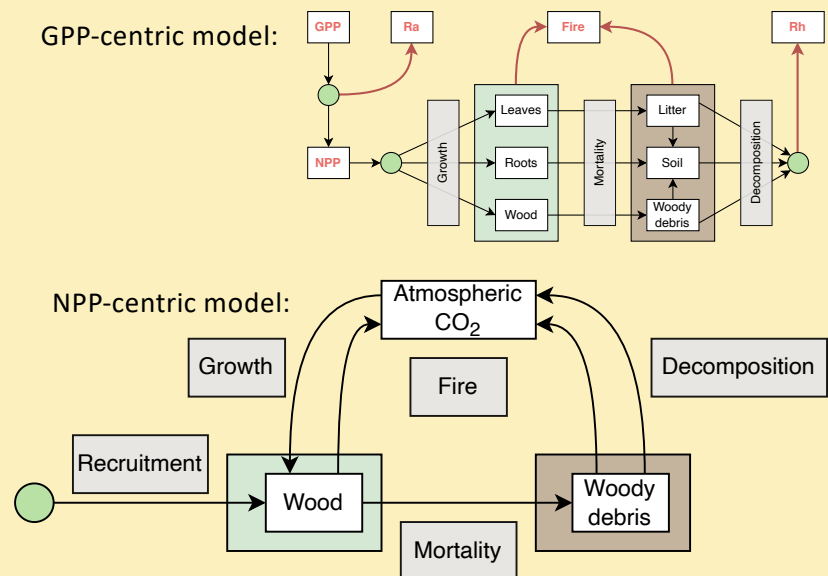
When we measure the carbon dynamics of forest ecosystems in the field, we generally do it with permanent sample plots. These are circles or rectangle patches of forest, within which we repeatedly measure every tree stem over a certain size over a number of years. We record the tree species, the stem diameter, the height of the tree, whether the tree is alive or dead, and potentially many other things that tell us about biomass contained in a tree, or the factors which might govern its growth rate and risk of mortality.

Stem diameter is most often measured with a tape measure at a particular height on the trunk, or sometimes with these things called dendro-bands, which more precisely measure the growth of a stem by stretching a spring.

To re-measure the same tree stems over time, we generally nail a metal tag into the stem which has a stamped number on it.

Zooming in: forest carbon fluxes

We can re-arrange the conceptual model to highlight the parts of the system we can measure.



So, given the data we have available, we can re-arrange this original model of the carbon cycle, which is centred around GPP, into a model that is centred around NPP, that is the production of woody biomass.

Here we have inputs to the woody pool as the recruitment of new stems, the growth of those stems, and the death of those stems.

Measuring growth from field measurements

Allometric equations (models) relate **diameter** and **height** measurements, and species **wood density** to biomass (Mg) for an individual:

$$B = 0.0673 \times (\rho \times H \times D^2)^{0.976} / 1000$$

ρ = wood density (g cm⁻³)

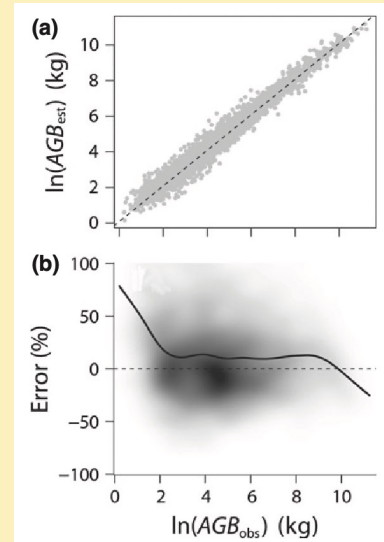
H = tree height (m)

D = stem diameter (cm)

Numeric constants derived by constructing a model from observed biomass measurements of harvested trees.

Biomass converted to carbon by conversion factor (x0.5).

Chave et al. (2014), Réjou-Méchain et al. (2017), Sillescu (2014)



In the field as I mentioned we record the diameter, height and tree species of each stem. We can use these measurements to estimate the biomass of the tree using something called an allometric model.

Allometric models are essentially an equation, an empirical model, which relate non-destructive measurements of trees to biomass. These models are calibrated by destructively harvesting many trees and measuring their biomass manually, which provides values for the numeric constants in the model.

I think you have heard about these before?

From the tree species we can get an estimate of wood density

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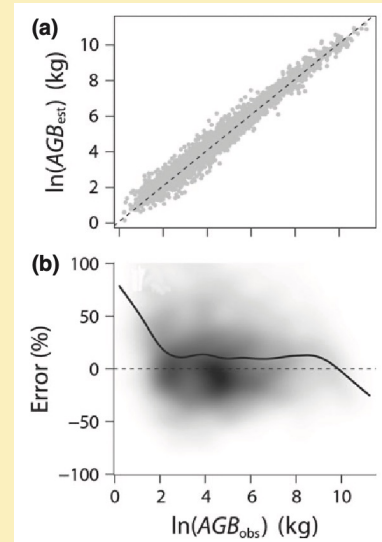
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For the rest of the session, I'll refer to biomass, but know that carbon is roughly half the biomass, by weight.

This allometric equation comes from a very famous study by Jerome Chave in 2014, and is used across the tropical region to estimate biomass.

We will use this allometry today in the practical.

There is uncertainty in this allometry, which is dependent on the size of the tree. Small trees tend to be over-estimated in their biomass, and large trees tend to be under-estimated. It's important for us to see whether our trees are large enough that this will pose a problem.

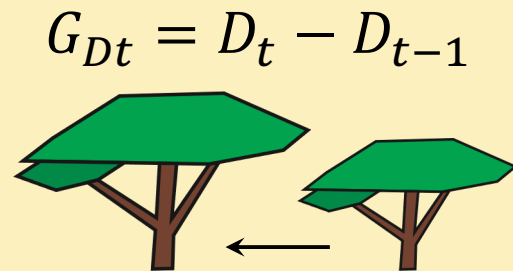
Measuring the growth of an individual

The simplest method of measuring growth:

- G_{Dt} = Diameter growth over the period $t - 1$ to t
- D_t = Diameter at t
- D_{t-1} = Diameter at $t - 1$

But:

- Only over a single period.
- Absolute change, not a rate.
- For a single individual we have no measure of uncertainty.
- Diameter \neq carbon ($B \times 0.5$)



Now we are going to talk about how we parameterise a model of forest growth.

Starting off very simply, we can track the diameter growth of a tree stem between two time points by subtracting the diameter at the first time point from the diameter at the second time point.

But, this only gives us a single estimate of growth over a single period.

It also only gives us absolute change, not a rate, which we need to make a general model about forest growth over time.

Also, diameter does not relate directly to carbon, or biomass.

The general rule is that carbon by mass is half the biomass.

Measuring the growth of an individual

Let's add a time term:

- G_D = diameter growth over the period $t - 1$ to t
- D_t = diameter at t
- D_{t-1} = diameter at $t - 1$
- T = census interval length

$$G_D = \frac{D_t - D_{t-1}}{T}$$

Now G_D is in units of D per T

Convert diameter to biomass with allometric model, then to carbon with conversion factor (x0.5).

So, to turn it into a rate we can simply divide by the length of time between time t and time $t-1$. Now our estimate of growth is in units of diameter per unit time. For forest models this is mostly in years.

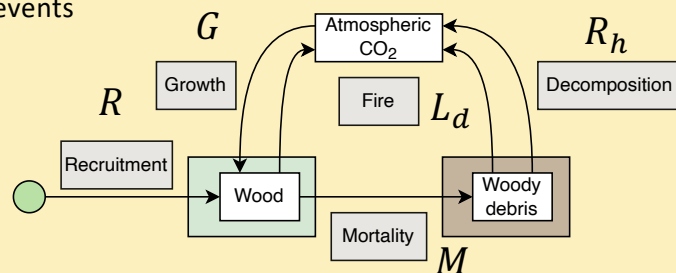
Measuring Net Biome Production (NBP)

NBP = Total net exchange of carbon between ecosystem and atmosphere.

$$NBP = GPP - R_e - L_d$$

- R_e = ecosystem respiration = autotrophic (R_a) + heterotrophic (R_h) respiration
- L_d = emissions from disturbance events

$$NBP = G + R - M$$



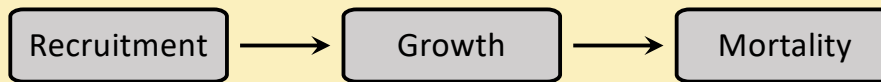
So that's how we can measure the growth at the level of a single tree.

Our ultimate goal is to model the total carbon sink effect of an entire forest ecosystem, not just one tree. The total net exchange of carbon between the ecosystem and the atmosphere is referred to as the Net Biome Production, or NBP. In a closed system, i.e. the planet Earth, we can assume that NBP is the sum of all the productivity by photosynthesis in the ecosystem, minus any losses by respiration or from disturbance events by fire.

In our model centred around field measurements of tree growth, we can also define NBP as all the growth and recruitment into the woody carbon pool, minus any losses due to tree mortality.

The big assumption we are making in our model is that over a long enough timescale all the carbon held in the wood returns to the atmosphere through decomposition and fire. This isn't the case in reality, there will be some carbon which stays in the soil or is exported out of the system e.g. as dissolved organic carbon in water.

Calculating rates of production and loss

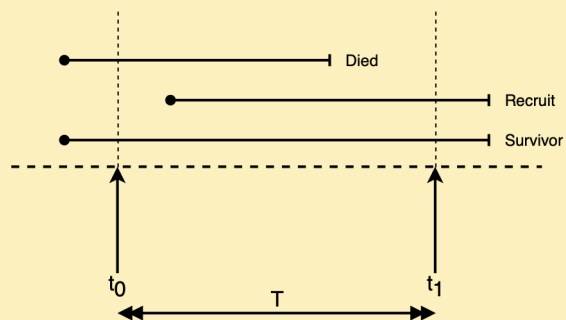


Simple production: $P_s = \frac{B_T - B_{s0}}{T}$

Simple loss: $L_s = \frac{B_0 - B_{s0}}{T}$

- Biomass at final census: B_T
- Biomass of survivors at first census: B_{s0}
- Biomass at first census: B_0
- Census interval (years): T

As the census interval increases, increase in unmeasured growth, which reduces estimates of P_s and L_s .



Kohyama et al. (2017, 2019)

Now I want to get onto using population-level measurements of woody biomass to parameterise an empirical model of forest productivity and loss.

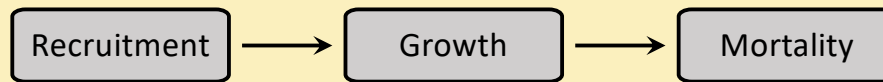
Production here could also be referred to as the biomass increment, or wood production, and encompasses the biomass added by new recruits as well.

When we're dealing with only two censuses, we can calculate production simply as the total biomass recorded in the final census, minus the initial biomass of all those stems which survived from the first census to the final census. Then divide this by our census interval to get a rate.

Similarly, loss can be calculated as the total biomass in the first census, minus the initial biomass of all the survivors divided by the census interval.

These estimates are biased

Calculating rates of production and loss

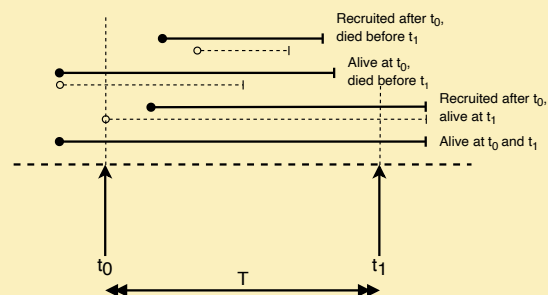


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Similarly, loss can be calculated as the total biomass in the first census, minus the initial biomass of all the survivors divided by the census interval.

These estimates are biased by census interval. As the census interval increases, we will have more trees which grow then die somewhere in the census interval, and similarly more trees which recruit and then die within a single census interval.

We can improve upon these simple equations by calculating them as instantaneous

rates ...

Calculating rates of production and loss



Instantaneous production:

$$P = \frac{\ln(B_T/B_{S0})(B_T - B_0)}{T \times \ln(\frac{B_T}{B_0})}$$

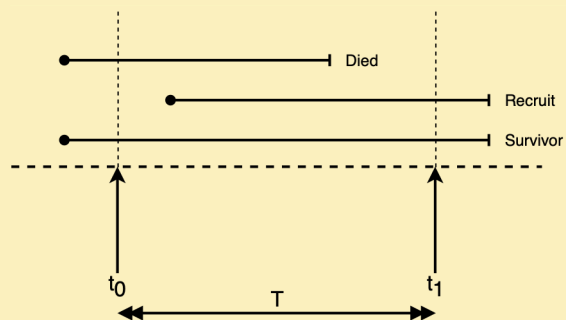
Independent of census interval.

AKA: logarithmic growth rate estimation

Instantaneous loss:

$$L = \frac{\ln(B_0/B_{S0})(B_T - B_0)}{T \times \ln(\frac{B_T}{B_0})}$$

- Biomass at final census: B_T
- Biomass of survivors at first census: B_{S0}
- Biomass at first census: B_0
- Census interval (years): T



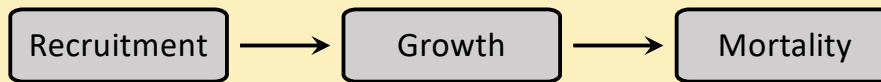
Kohyama et al. (2017, 2019)

These instantaneous rates are also referred to as logarithmic growth rates.

Not enough time to show you how these rates are derived, but know that they help to remove that bias caused by increasing census interval.

If you want to read more about these methods, see Kohyama et al. 2019 in particular

Calculating rates of production and loss



Intrinsic rate of change (r):

$$r = \ln\left(\frac{B_T}{B_0}\right)/T$$

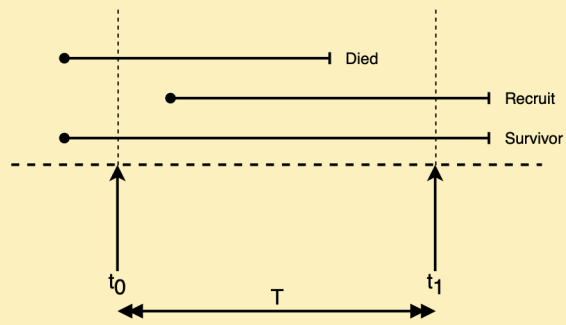
If $r > 0$, biomass **increasing**.

If $r < 0$, biomass **decreasing**.

Rate of net biomass change ($\delta B/\delta T$):

$$\delta B/\delta T = P - L = P_s - L_s = P_{ann} - L_{ann}$$

$$\delta B/\delta T = G + R - M = NBP$$



Kohyama et al. (2017, 2019)

Further, we can calculate other metrics to describe the biomass dynamics of a system.

The intrinsic rate of change is calculated as the natural log of final biomass over initial biomass divided by time. This metric is valuable as it gives us a simple measure of whether biomass is increasing or decreasing. It is sometimes referred to as the intrinsic rate of increase in population and community ecology.

Similarly, we can also calculate the rate of net biomass change as the production rate minus the loss rate. If dB/dT is positive, biomass is increasing, if negative, decreasing.

r is a proportional increase, while dB/dT is in units of biomass per unit time.

Getting back to our original goal of measuring NBP, dB/dT is also equal to all the growth and recruitment fluxes minus the mortality flux, which is the same as NBP.

Deriving other metrics

Average biomass residence time: $B = B_T / f_{mort}$

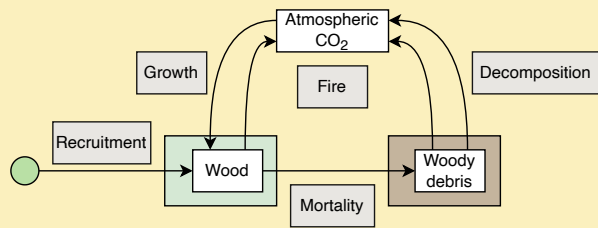
Mean period biomass: $B_w = \frac{B_T - B_0}{\log(\frac{B_T}{B_0})}$

Flux to dead wood pool: $f_{mort} = B_0 - B_{s0}$

Species or size-class specific growth, mortality risk and recruitment rates.

Per area growth rates (divide by plot area)

Forecasted biomass production



Koven et al. (2015), Kohyama et al. (2018)

On top of that, we can measure the rate at which biomass travels through our system as the average biomass residence time,

Or the mean biomass over the period of the census measurements.

We can also help to parameterise our conceptual model of carbon fluxes in the ecosystem by calculating the flux to the dead pool.

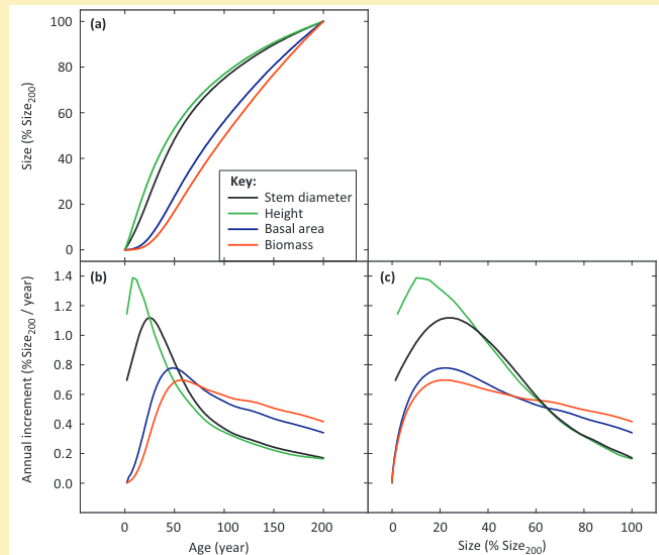
Species and size-class specific vital rates

Growth rates differ with tree size and species.

Simple to subset population and calculate rate of production / mortality for each species or size class separately, assuming sufficient sampling effort.

Can apply these rate estimates to new communities.

More on this in the practical...



Bowman et al. (2013)

We can add more detail to our model of forest biomass dynamics by understanding that there is heterogeneity within tree populations that leads to variation in their rates of production and mortality.

This plot shows that as trees get older and larger they generally grow slower.

We can subset the population we measure and calculate rates of production and loss for different size classes.

Species and size-class specific vital rates

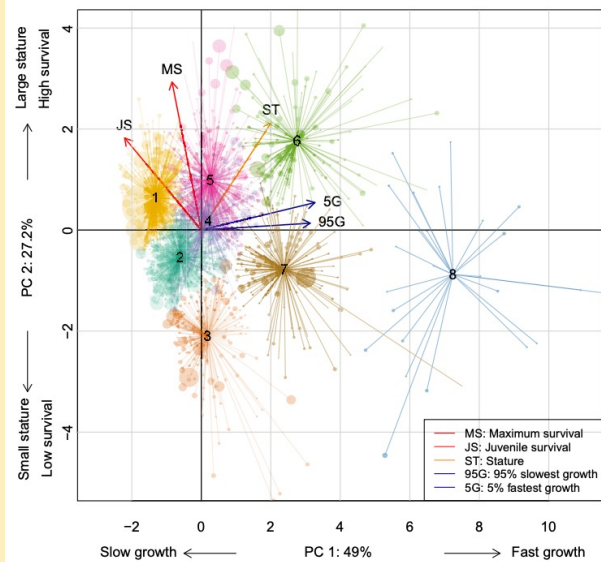
Growth rates differ with tree size and species.

Simple to subset population and calculate rate of production / mortality for each species or size class separately, assuming sufficient sampling effort.

Can apply these rate estimates to new communities.

- 1 Very slow-growing
- 2 Slow-growing, low survival
- 3 Very low survival
- 4 Intermediate growth and survival
- 5 Large statured, high survival
- 6 Very large statured, fast growth
- 7 Fast growth, low survival
- 8 Pioneers—very fast growth

Needham et al. (2022)



We also know that growth rates differ with tree species. Tree species vary in their life history strategy, i.e. how they grow and remain competitive with other species. This graph shows a principal component analysis of tree species from across the world that have been separated into groups based on their growth rate, survival rate, and maximum size. There is lots of variation.

We can subset the population based on species or other taxonomic groupings.

These species specific estimates can then be applied to new communities.

By incorporating these more complex elements we are making our model more general and realistic, but at a cost of needing more data to parameterise the model.

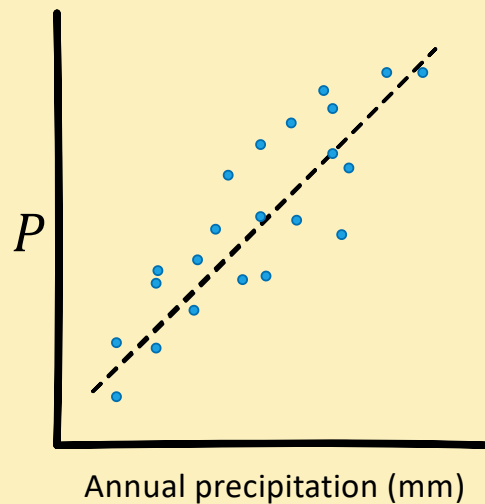
Identifying drivers of biomass change with statistics

We can identify extrinsic and intrinsic drivers of growth, mortality, recruitment, using simple statistical analyses.

E.g. linear regression of Mean Annual Precipitation (MAP) and wood production rate (P).

E.g. logistic regression of mortality likelihood with drought intensity.

This can help us to predict these vital rates in unmeasured ecosystems.



Now that we have all these metrics derived from our empirical model which describe the forest ecosystem and its carbon dynamics, we can use simple statistical analyses to try and understand why these metrics might vary among ecosystems.

For example, we expect that woody production rate will increase with water availability, as more water allows greater rates of photosynthesis. We could do a simple linear regression of these variables to see if there is any real effect.

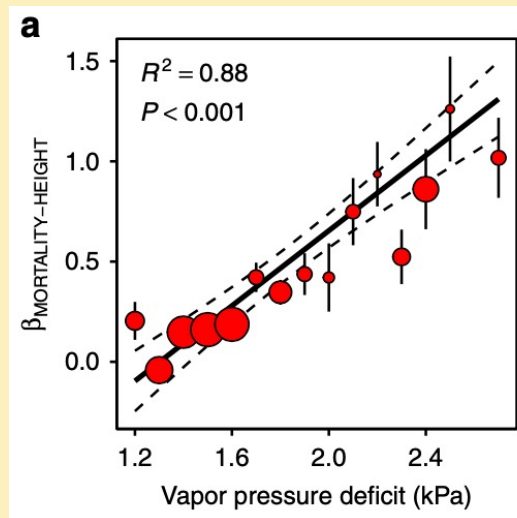
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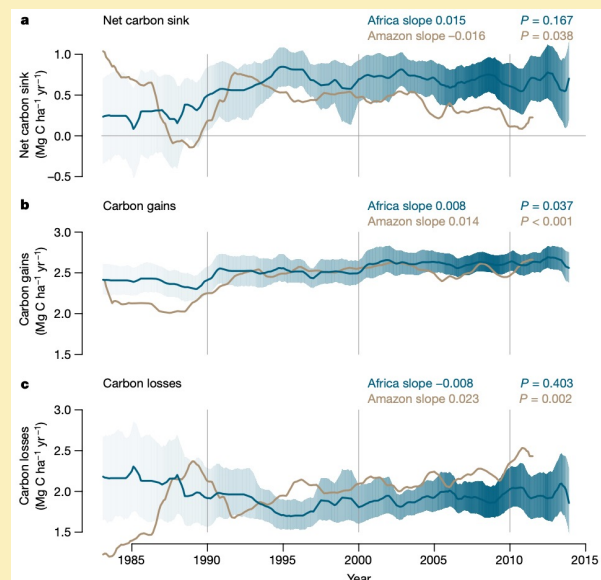
Stovall et al. (2019)

Similarly, as vapour pressure deficit (dryness of the air) increases, large trees become increasingly at risk from drought induced mortality. We could do a logistic regression to predict how mortality rate increases with drought intensity.

In practice: carbon dynamics in wet tropical forests

- Comparison of African (Congo) and South American (Amazon) wet forests, using field data from plots.
- Net carbon sink is declining in the Amazon, but is stable in Africa.
- Amazon sink is declining in Amazon because of increased mortality. Growth remains stable.

Hubau et al. (2020)



Here are a couple of examples which show how these sorts of empirical models have been applied in real research.

This paper used measurements from many plots across wet forests in Africa and South America.

They estimated rates of carbon gain and loss using empirical models very similar to the ones I have talked about above, and which you are going to run in the practical.

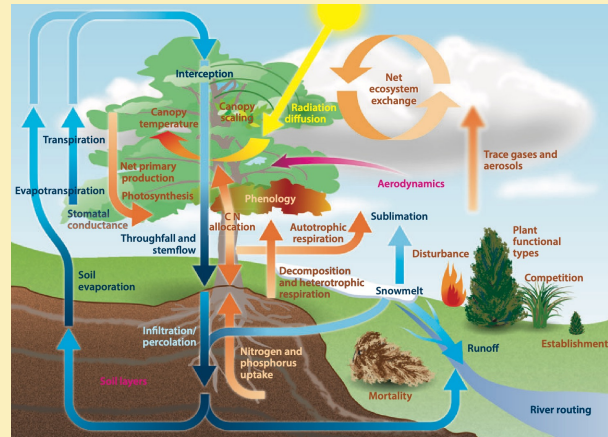
They found that the carbon sink effect is decreasing in the Amazon, and that this is due to increasing mortality (loss rate), rather than a decrease in productivity. In Africa however, they found that the sink was remaining stable.

They used a model to describe a system and this raises more questions about why this might be happening. To do this next bit of research, they might choose a more mechanistic approach.

In practice: forest dynamics in earth system models

DGVM - Dynamic Global Vegetation Model

- Mechanistic models of vegetation growth, response to climate, soil, disturbance.
- Combines biogeography, biogeochemistry, biophysics, and vegetation dynamics.
- A component of larger Terrestrial Biosphere Models (TBMs), which model global biogeochemical cycles
- DGVMs require parameterization using observed data.



More on this in Luke Smallman's module!

Fisher et al. (2014, 2017)

Empirical models of forest growth and mortality are also used in mechanistic models of the global carbon cycle, to parameterise the response of forests to climate change, and to measure variation in forest behaviour across vegetation types.

Dynamic Global Vegetation models combine information on biogeography, biogeochemistry, biophysics and vegetation dynamics to understand the carbon dynamics of forests in response to climate change.

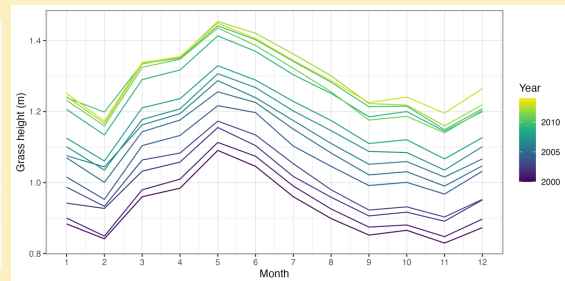
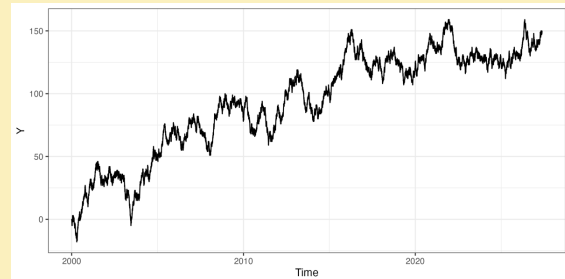
Luke will cover this much more later on.

What do we know?

- Empirical modelling != mechanistic modelling.
- Allometric equations relate non-destructive field measurements to biomass, but carry their own uncertainty.
- Field measurements can be used to model net biome production.
- We can make sensible assumptions to estimate unseen productivity.
- With a structural model we can estimate unmeasured carbon fluxes.
- With sufficient sampling, we can build more complex models of forest dynamics by calculating growth/mortality/recruitment rates across size classes and species.
- Using basic statistics we can relate vital rates to potential environmental drivers of biomass change.

Next time...

- Time series analysis
- Population modelling
- Spatial simulation



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Practical

Go to Learn:

- i. Modelling Ecosystem Processes
- ii. Module 3 - Forest Biomass Dynamics
- iii. Week 5

Download all the files to a single folder

EXTRA SLIDES

Estimating unmeasured growth and mortality

Recruits which died before t_1 : U_r
 N unobserved recruits = $N_0 \times M \times R \times T$

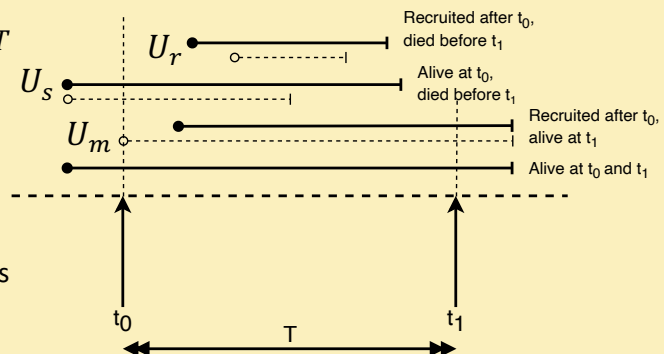
- Number of stems at t_0 : N_0
- Annual mortality rate: $M = \ln(\frac{N_0}{N_{S_0}}) / T$
- Annual recruitment rate: $R = \ln(\frac{N_T}{N_{S_0}}) / T$
- Census interval (years): T

Assume growth rate and wood density of U_r as plot level mean of small stems.

Assume U_r stems recruit in 1/3 into census interval and die 2/3 into census interval.

Unobserved survivors: U_s
 Assume death at midpoint of census interval

Unobserved recruits: U_m
 Assume grew from 0 at t_1



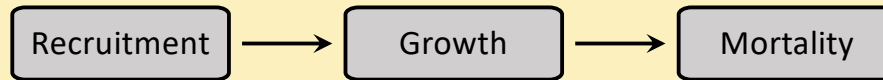
Talbot et al. (2014)

$N_{\{T\}}$ = number of stems at final census

$N_{\{0\}}$ = number of stems at first census

$N_{\{S_{\{0\}}\}}$ = number of survivors from first census found in final census

Calculating rates of growth and loss



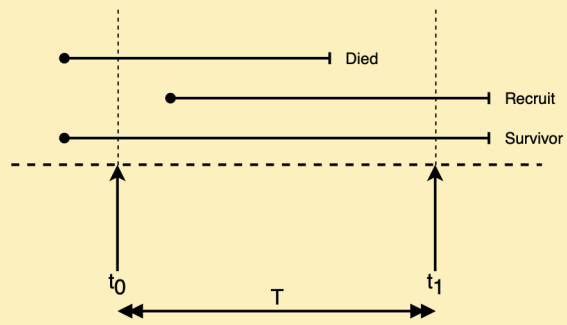
Annual production:

$$P_{ann} = \left(\left(\frac{B_T}{B_0} \right)^{1/T} \right) \times \left(1 - \left(\frac{B_{s0}}{B_T} \right)^{1/T} \right)$$

Annual loss:

$$L_{ann} = \left(1 - \left(\frac{B_{s0}}{B_0} \right)^{1/T} \right)$$

- Biomass at final census: B_T
- Biomass of survivors at first census: B_{s0}
- Biomass at first census: B_0
- Census interval (years): T



Kohyama et al. (2017, 2019)