Carbon flux & climate change in the tropics

Overview of primary productivity and carbon fluxes

Consider variation in carbon sinks across the tropics

(Begin to) discuss complex effects of rising temperatures

Preview and definitions

Primary productivity: the total amount of carbon fixed as organic matter in the process of photosynthesis, usually measured as net primary productivity (NPP), the amount of carbon devoted to growth and reproduction

Carbon flux: the rate at which carbon enters and leaves ecosystems

- If more carbon is stored in plant biomass (more enters by photosynthesis) than what leaves (metabolic respiration), then the plant community acts as a *carbon sink*
- If the opposite happens, we have a *carbon source*

Preview and definitions

Net ecosystem productivity (NEP): the amount of carbon added after accounting for carbon losses from respiration by plants, all consumer animals and all decomposers

Why it is complicated:

Tropical forests are sensitive to changes in annual temperature, drought and precipitation, which can result in shifts in biomass accumulation, tree recruitment, species composition and decomposition rates, all of which affect carbon flux.

Concepts to keep in mind:

1) *Tropical forests are normally high in NPP, and can potentially gain carbon added to the atmosphere by human activities*
2) *Studies show that regions differ in the degree of carbon sequestration, and we still do not know how tropical forests will respond to climate change with regard to carbon flux*
3) *This is one of the more complex topics that tropical ecologists are facing*

Primary productivity

Primary productivity is the total amount of carbon fixed as organic matter in the process of photosynthesis, usually measured as net primary productivity (NPP), the amount of carbon devoted to growth and reproduction.

Tropical forests accomplish more photosynthesis than any terrestrial system

- 1 ha of rain forest is more than twice as productive as a ha of northern conifer forest

Tropical forests cover 7-10% of global land area and stores 40-50% of carbon present in terrestrial systems

NPP can be measured by weighting biomass change over a period of time

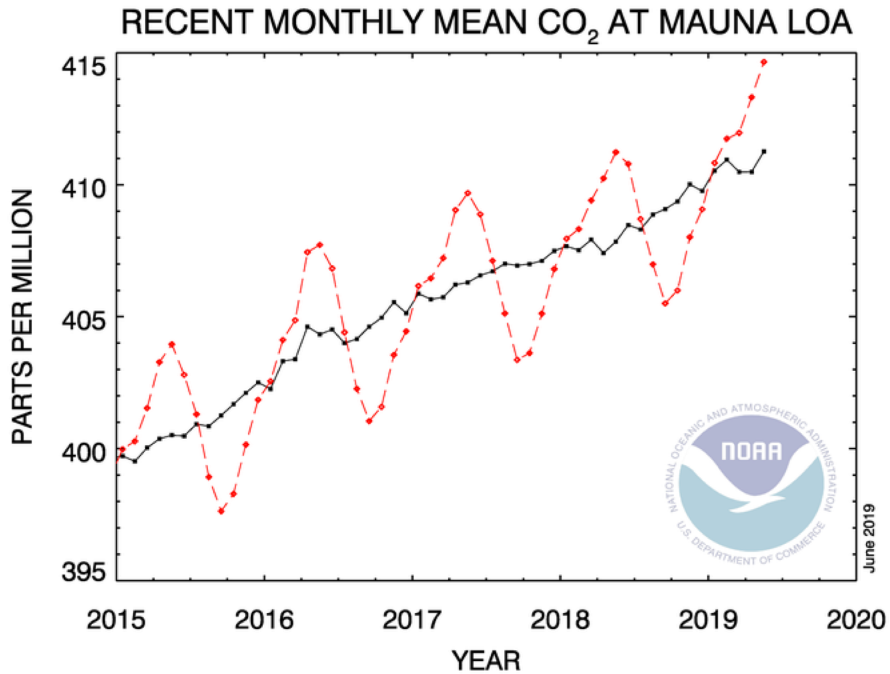
$$6CO_2 + 6H_2O \xrightarrow[\text{Nutrients}]{\text{Sunlight}} C_6H_{12}O_6 + 6O_2$$

Organic compounds

Malhi & Grace 2000, *TREE*

Primary productivity

Atmospheric carbon dioxide has been increasing since the Industrial Revolution and continues to rise



Tropical forests have the potential to store a great amount of carbon in biomass, which could mitigate carbon dioxide increases in the atmosphere – but tropical forests are also metabolically active, so we must also understand how much carbon is released from tropical forests during normal metabolism.

Rain forest NPP in global context

Tropical humid forests demonstrate the highest net primary productivity of any terrestrial ecosystem, but there is more to the forest than the trees.

All organisms in the forest are emitting emit carbon dioxide as they respire: animals, plants, decomposers

Carbon flux depends on NPP of all plants as it relates to total respiration of all plants, consumers and decomposers:

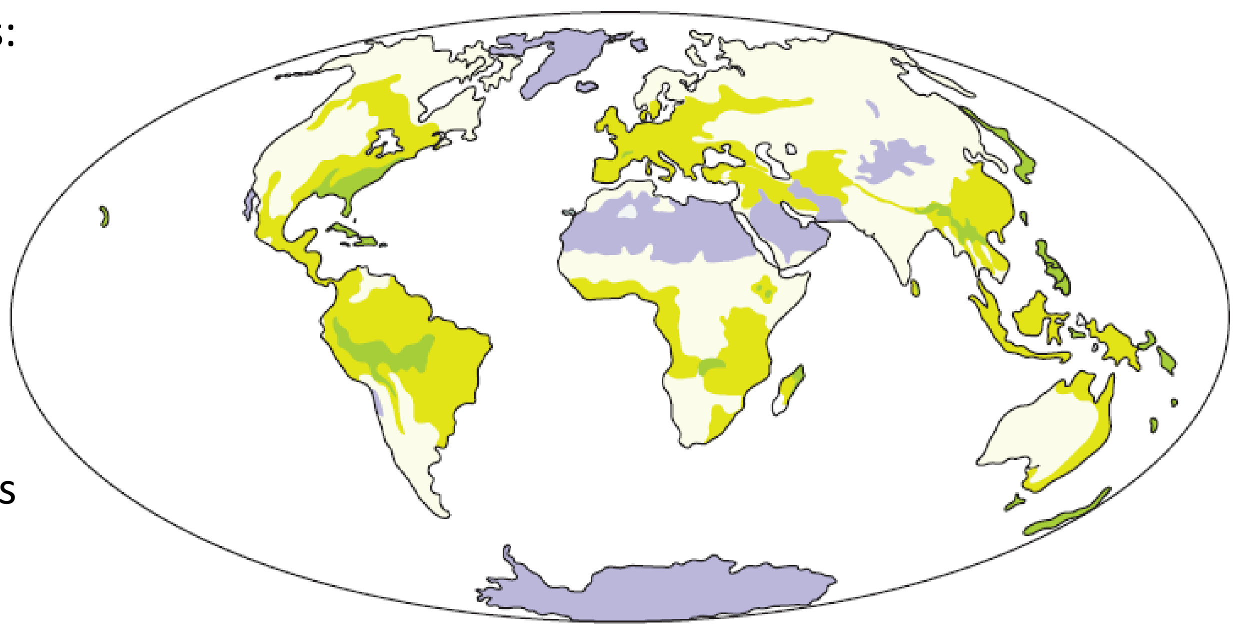
Net Ecosystem Productivity

NEP = NPP – R – R – R

plants

consumers

decomposers

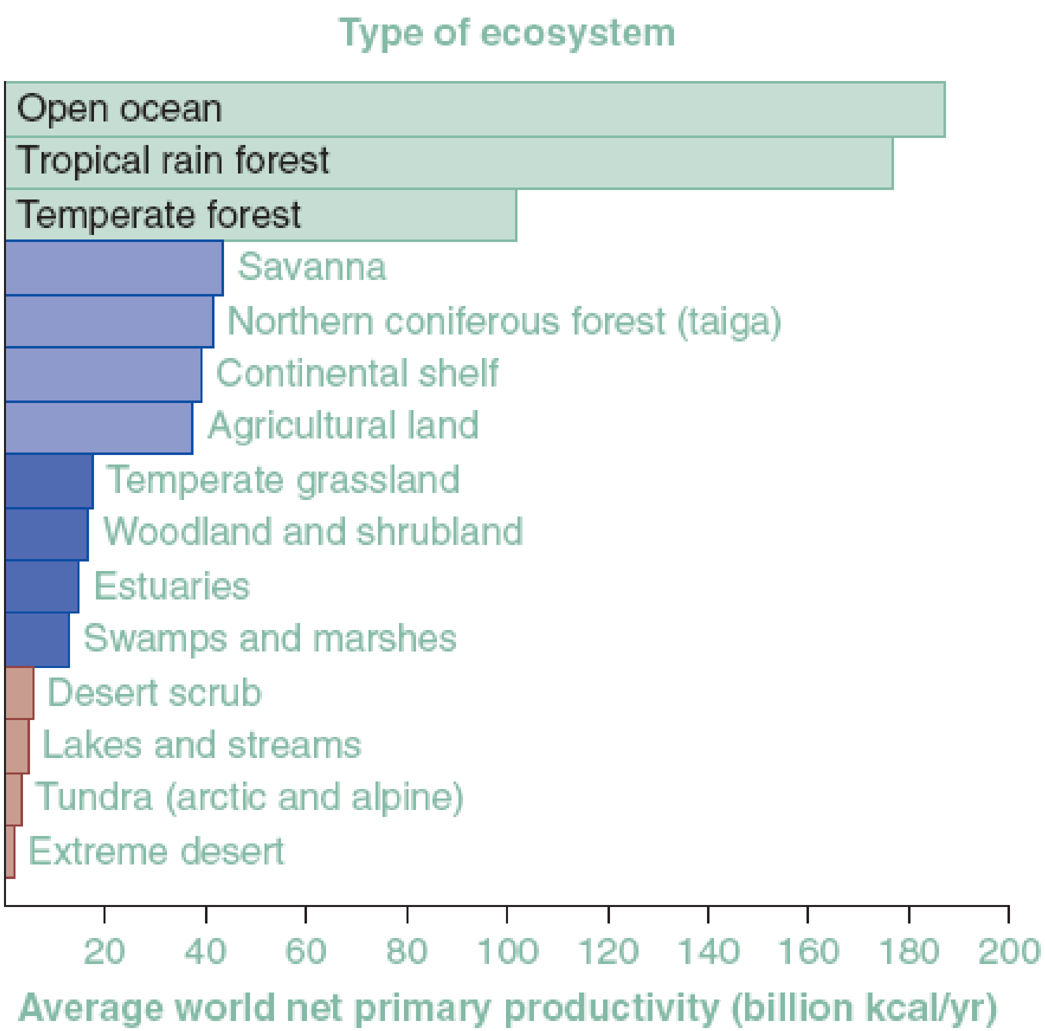


Map of global net primary productivity (NPP)

Rain forest NPP in global context

NPP of different ecosystems reflected in total area

Open ocean, though with vastly more area than tropical rain forest, barely exceeds it in global NPP



Rain forest NPP in global context

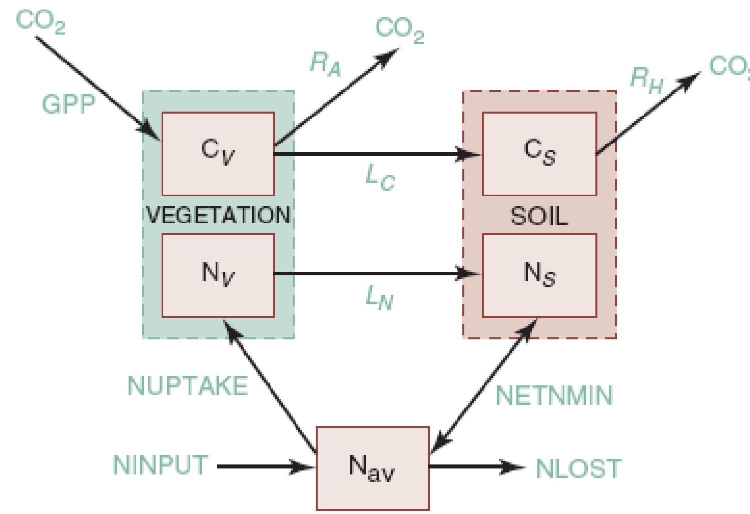
When forest is cleared, burned and converted to agriculture or pasture, there is much less biomass available for carbon absorption

High productivity of tropical forest is facilitated by a much longer growing season than in the temperate zone. (At the height of growing season, NPP of a temperate forest can be similar to a tropical forest)

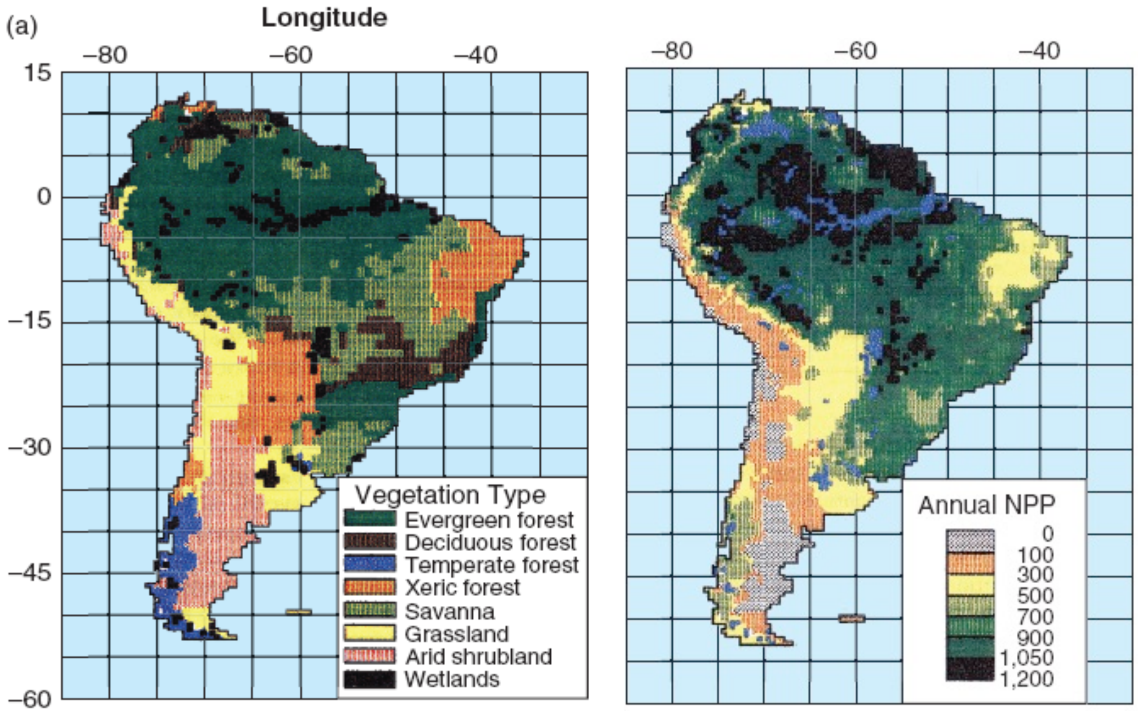
Tropical forests store 46% of global living terrestrial carbon and 11% of global soil carbon

Terrestrial Ecosystem Model

Model uses 5 state variables: carbon in vegetation C_v and soils C_s, nitrogen in vegetation N_v in soils N_s, and available soil inorganic N



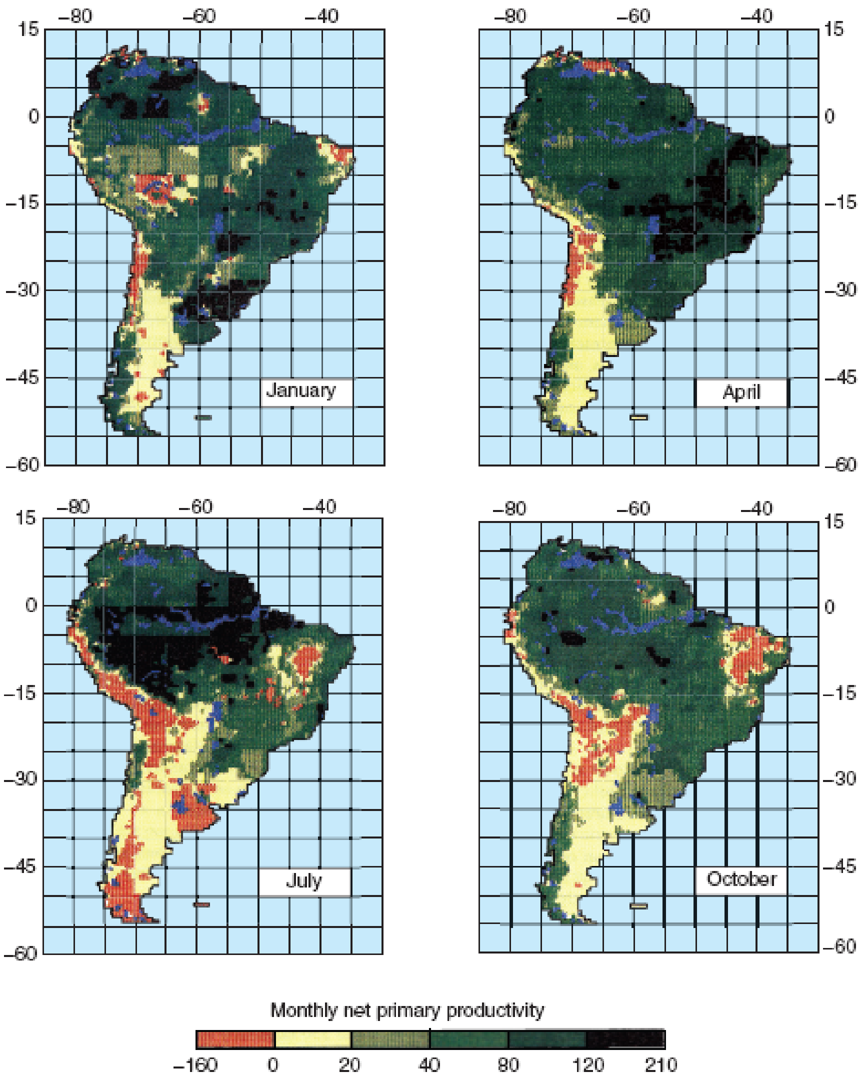
Calibrated using data from 12 sites around the world where NPP is known.



Shows that vegetation types highly correspond to NPP

~30% difference between the least and most productive ecosystems in South America

Terrestrial Ecosystem Model



NPP also showed strong patterns in seasonality, correlating to evapotranspiration

Values in red show higher respiration than primary production

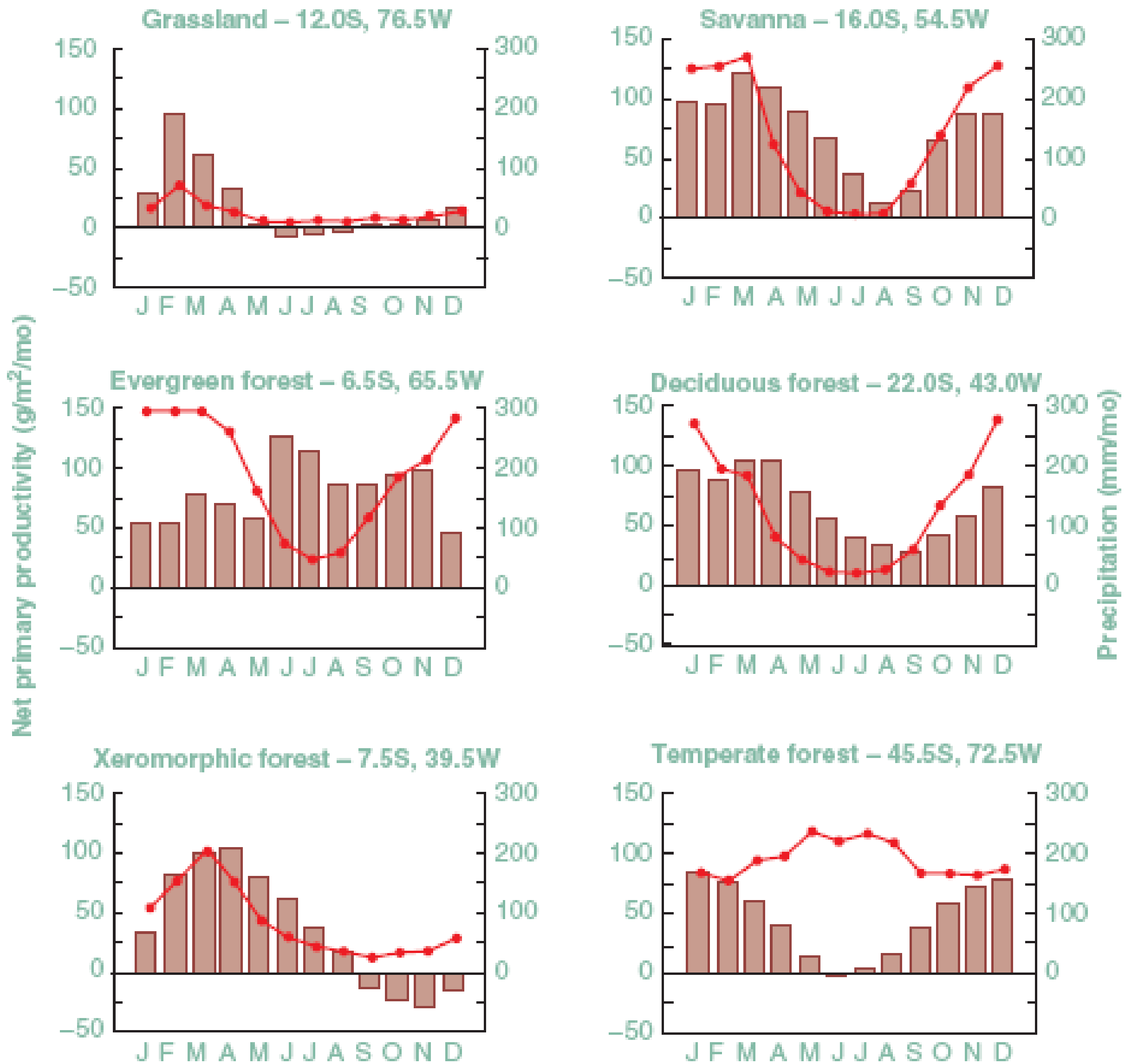
Solar radiation also influenced NPP seasonality, but radiation depends on cloud cover, which varies seasonally

NPP in the Amazon basin is seasonal due to variance in cloud cover

Terrestrial Ecosystem Model

NPP of savannas, tropical deciduous forests and dry forests correlate most strongly with mean annual soil moisture

In these areas, cloud cover is less of a factor, and in drier regions, rainfall is very important to NPP



Storing carbohydrates for a "sunny day"?

Many tropical plants spend most of their lives in the understory shade

How do they capitalize on opportunities for growth?

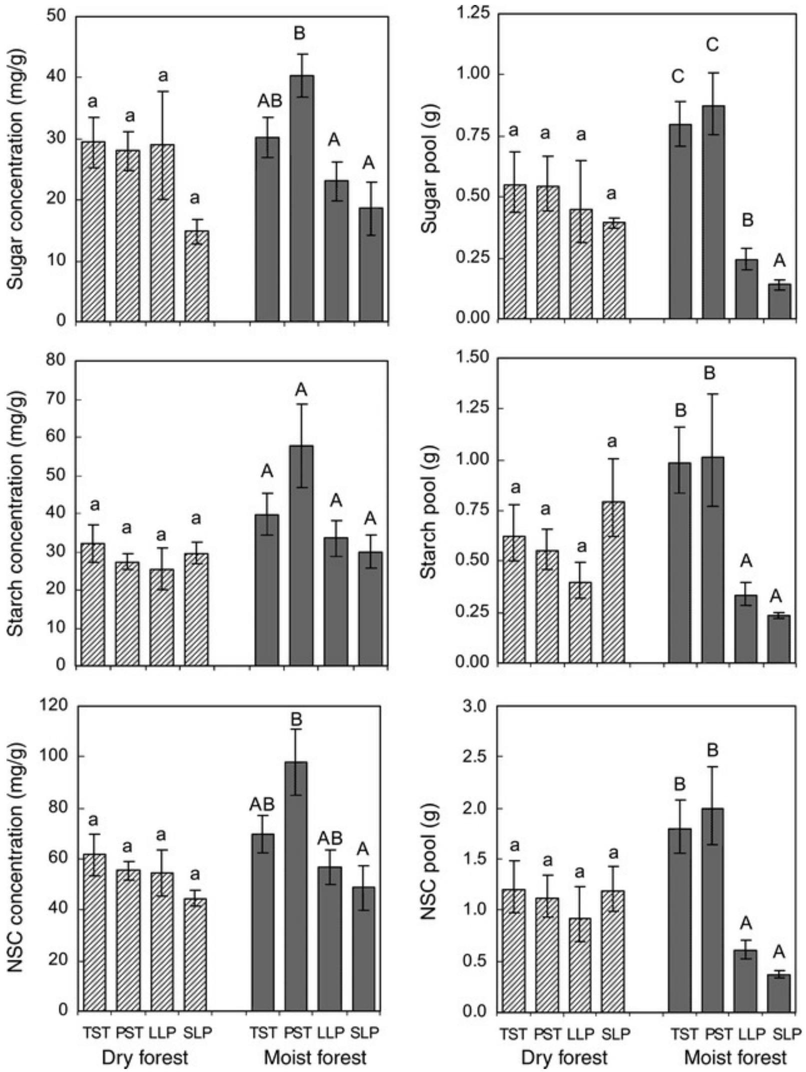
Must allocate investment to 1) utilizing carbon for growth or 2) for defense and storage

Nonstructural carbohydrates (NSC) are starches and sugars stored in plants that can be mobilized

Do some species have more stored NSCs than others?

Poorter & Kitajima 2007

Storing carbohydrates for a “sunny day”?



Study in Bolivia found that saplings in moist forest had higher NSC concentrations than those in dry forest

Suggests importance of storing carbs in trees occupying habitats with persistent shade (e.g., moist forest interior)

Tree species in different functional groups: TST = total shade tolerant; PST = partial shade tolerant; LLP = long-lived pioneers; SLP = short-lived pioneers

Among moist forest species, total shade tolerant (TST) and partial shade tolerant(PST) species stored the most carbohydrates

PST may have higher NSCs so they can be utilized to grow rapidly when a forest gap arises

Poorter & Kitajima 2007

Carbon Sinks: What are they?

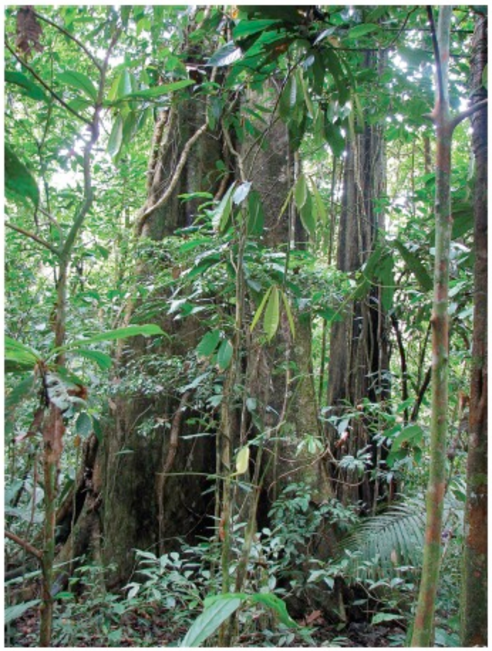
If movement of carbon into and out of a system is equal, the system is in equilibrium (rarely the case)

Growing ecosystems add carbon in biomass (more carbon removed from atmosphere than released back by respiration)

E.g., secondary succession adds carbon to biomass over time

Carbon sinks can also happen if more resources (CO2, H2O) permit higher rates of primary production that exceed rates of mortality and decomposition

Are tropical forests carbon sinks?



Proposed that with atmospheric increases in CO_2, oceans and lowland tropical forests act as carbon sinks, storing additional carbon released by fossil fuel burning and deforestation

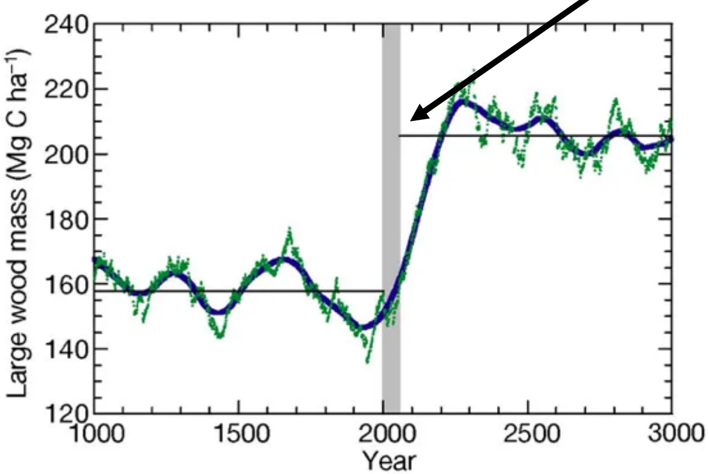
Terrestrial systems sequester 20-30% of carbon emitted annually as CO_2 – how much of this goes into rainforests?

This is not an easy question to answer…

Are tropical forests carbon sinks?

Carbon stored in wood/trunks/branches represents ~45% of total carbon storage in the tree, with mean residence time of ~80 years

One study investigated the response of large-wood carbon storage to a 25% increase in production distributed over 50 years for a 100-ha plot

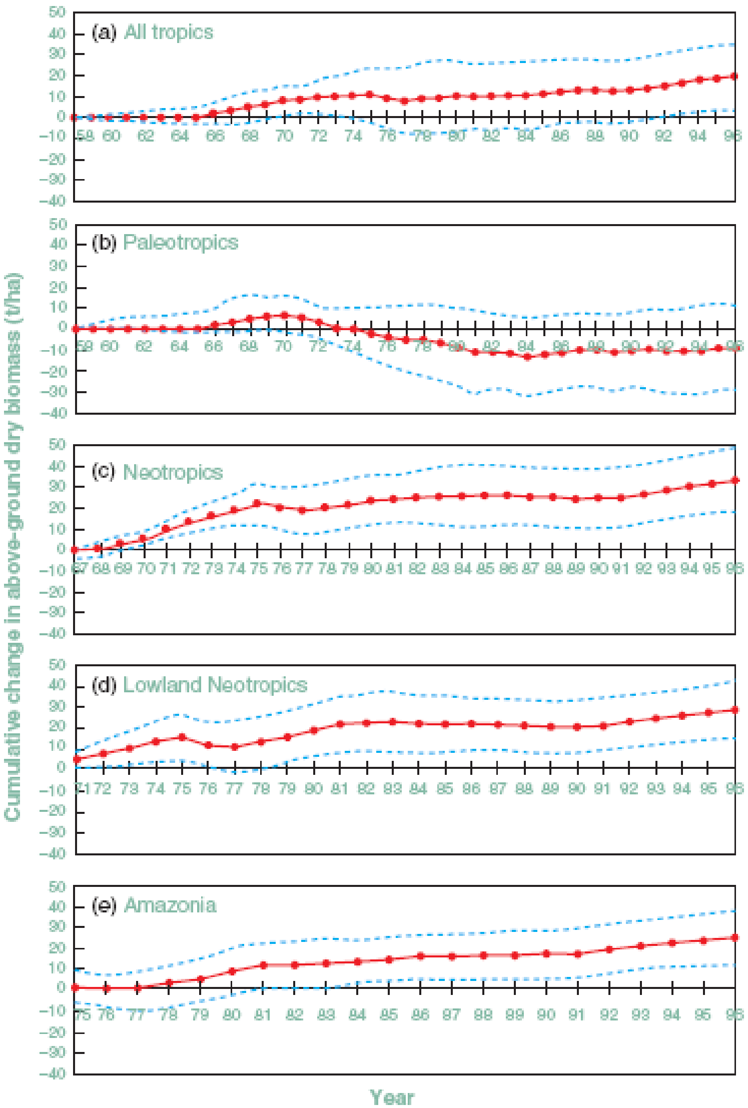


Carbon accumulated during years of increasing productivity, but once the productivity increase stopped, large wood continued to accumulate carbon for over a century

With a given increase in productivity (e.g., added atmospheric CO2), large-wood carbon storage will exhibit a lengthy lag time – Amazon forests could act as an important carbon sink

Chambers et al. 2001, Nature

Tropical forests as carbon sinks



A long-term study of the permanent forest plots globally found that biomass production exceeded losses from tree death at most sites

Measured basal area of >600,000 trees from 153 plots across the tropics

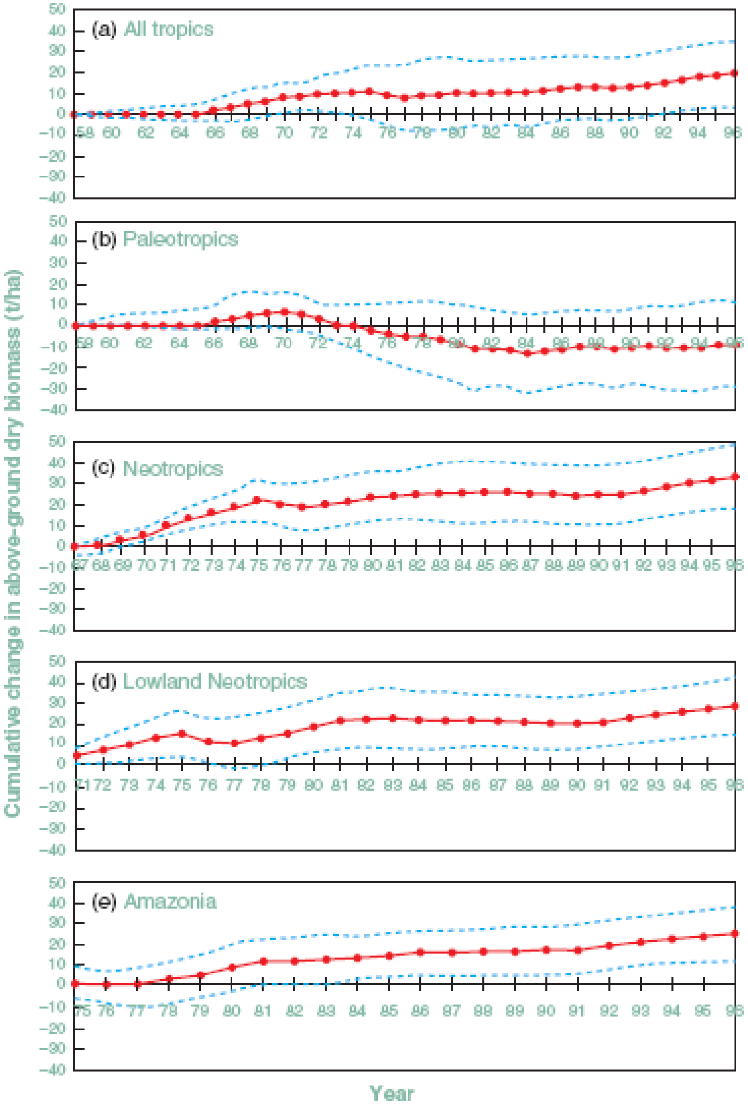
Measured mean rate of change across sites based on initial and final census

Estimated basal area change as a function of calendar year and were able to derive regional accumulated biomass over time

All sites in the Neotropics showed increases in biomass

Phillips et al. 1998

Tropical forests as carbon sinks



Possible (non mutually exclusive) explanations:

- Biomass is increasing with continental-scale cyclical climate change (ENSO events)

- Ecosystems are recovering from past widespread historical disturbance

- Biomass is increasing due to global climate change or additional resource availability (e.g., added CO2)

Phillips et al. 1998

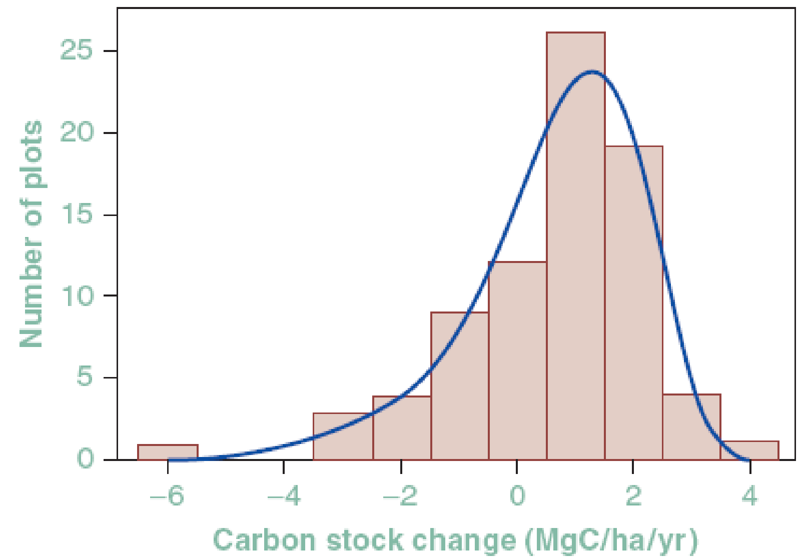
African forests as carbon sinks?

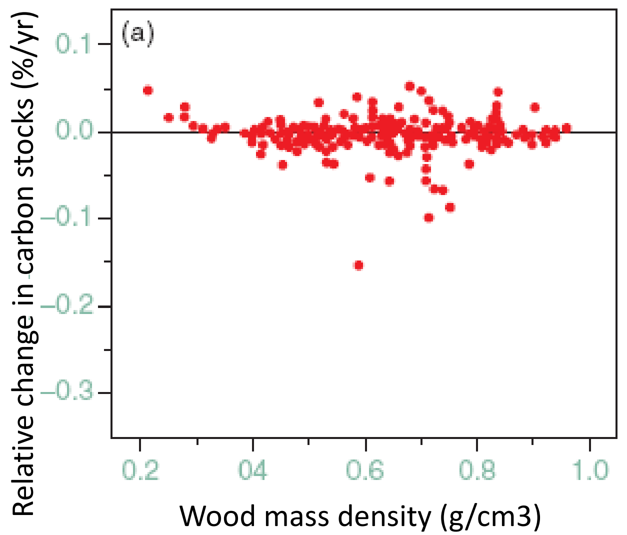
The Phillips et al. (1998) study showed the Paleotropics did not show cumulative change in above-ground biomass, like the Neotropics (but had few sites in the Paleotropics)

Another study, however, showed that African forests may also act as a carbon sink

79 long-term plots across 10 countries in Africa show that most plots are accumulating carbon in above ground storage

(This study did not account for potential carbon losses in areas due to forest harvesting or burning)





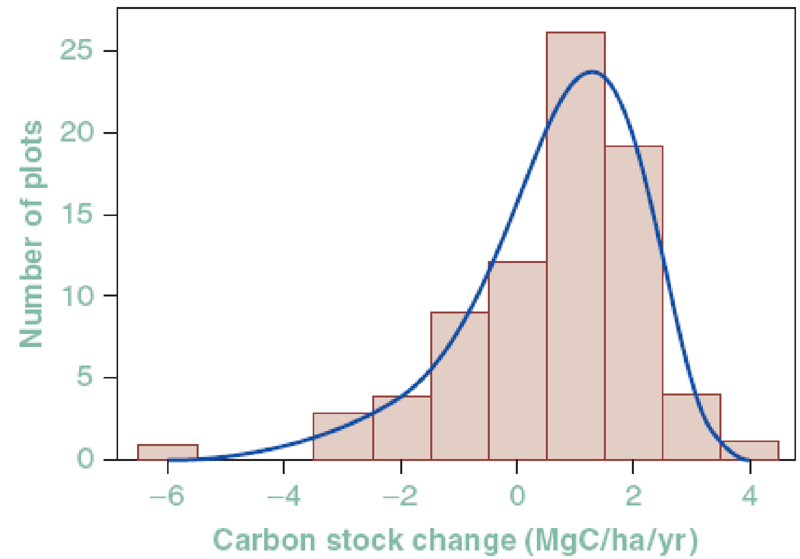
Lewis et al. 2009, Nature

African forests as carbon sinks: succession or fertilization?

Study tested to see whether carbon could be increasing due to:

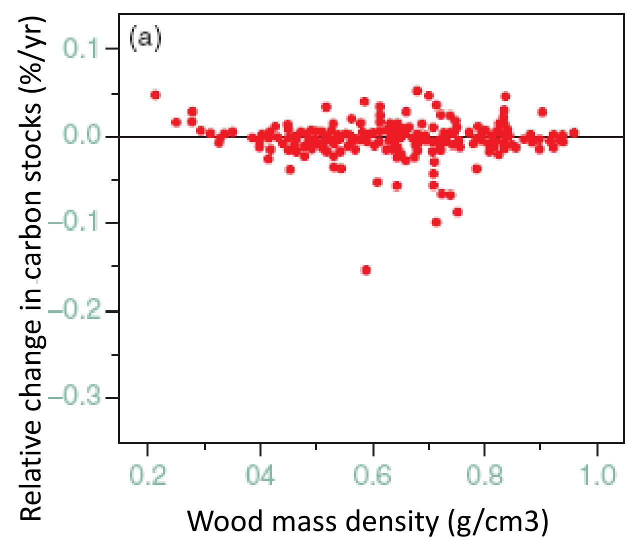
1) The forest not being in equilibrium (undergoing slow ecological succession following drought, fire, human use)

2) Fertilization by increased atmospheric CO2 and carbon sequestration



Compared tree species with lower wood mass density (typical of early succession) with species of high wood mass density (typical of late succession) – but found *no trends*

All stands were experiencing carbon increases regardless of successional histories – suggests that forests are indeed acting as carbon sinks in response to increased CO2



Lewis et al. 2009, Nature

Landscape effects on carbon sinks

Yet, the overall hypothesis that global forests are carbon sinks and gain biomass has found mixed support:

-Some forests appear to be gaining carbon, but only due to gap-phase dynamics (local disturbances within old forest were responsible for biomass gains)

-Idiosyncratic factors muddy the patterns (changes in temp, precip, cloud cover, anthropogenic pressures)

-Mortality events, which tend to be omitted, actually cause areas to be carbon sources

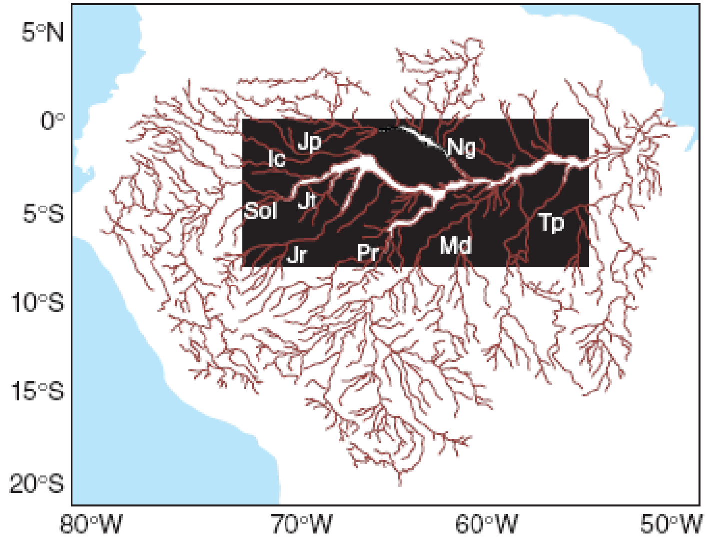
-Other studies found that only in La Nina years do forests really gain carbon

-The stage of the forest may affect the degree to which it is a carbon sink

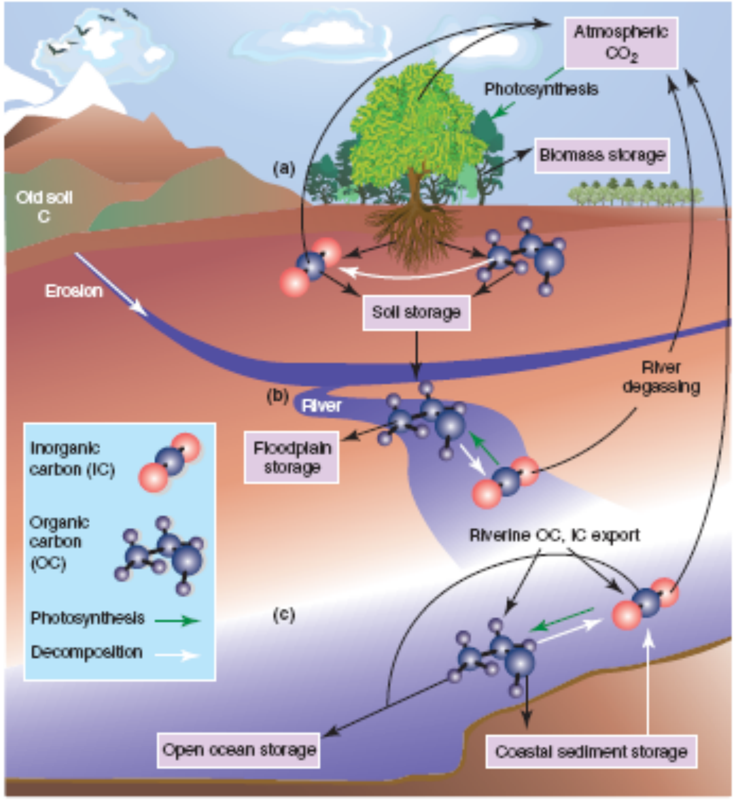
Early successional areas can add biomass quickly with short-lived species that grow rapidly, but longer-lived species can gain just as much carbon by persisting over a longer time frame.

Carbon loss and rivers

We've been suggesting that through biomass accumulation, tropical forests are experiencing a net gain of carbon, but these estimates are based on terrestrial measures… rivers offer their own system of carbon fluxes, and the metabolism of river systems affects overall carbon flux



Rivers and tributaries make up a large portion of the Amazonian basin



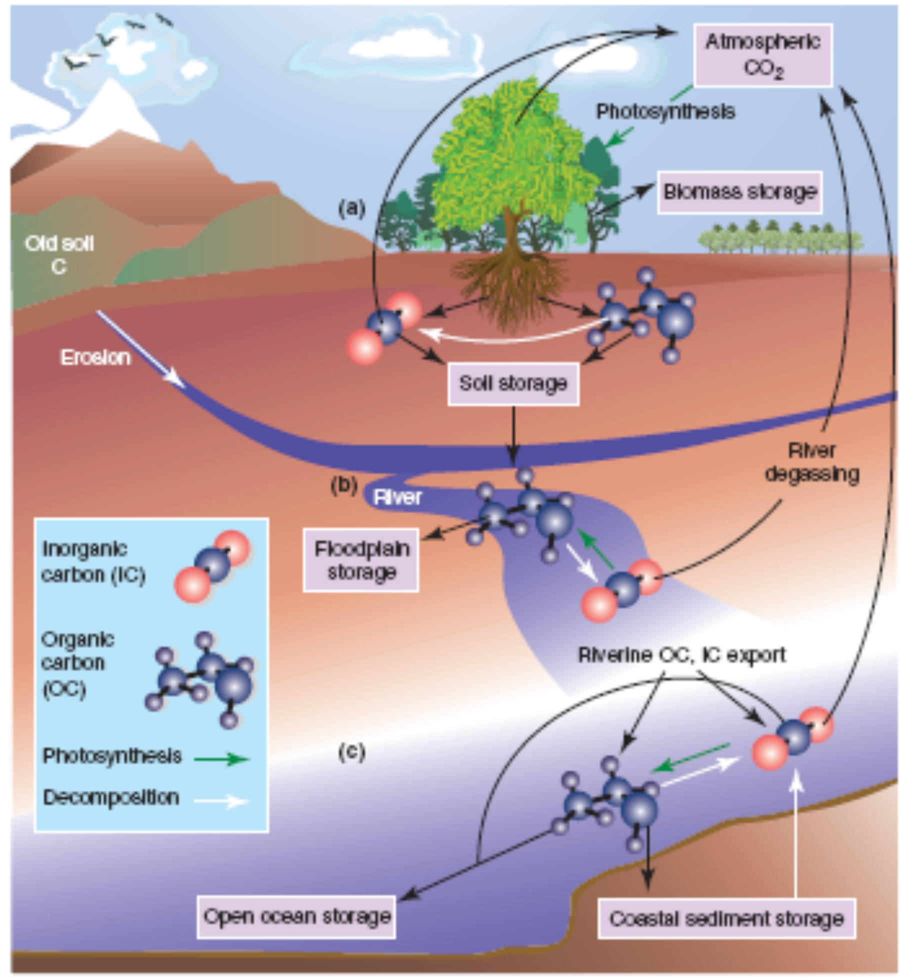
Carbon loss and rivers

Organic material entering rivers is an energy source for decomposers (fish to bacteria), which liberate carbon

Rivers also contain primary producers that fix carbon

Outgassing may represent a net loss of carbon through riverine metabolism

This may suggest that Amazonian lowland forests are not as effective as carbon sinks as we presume?



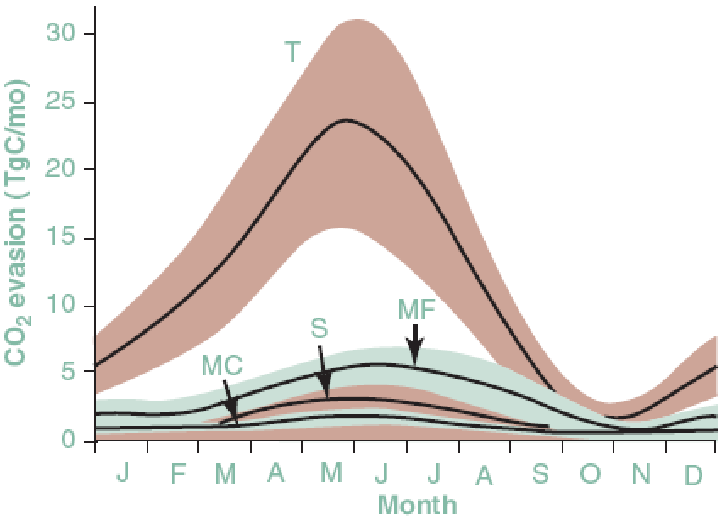
Carbon loss and rivers

A study looking at carbon flux in rivers in central Amazonia found that a large net amount of carbon is lost via outgassing

Rivers are not in carbon equilibrium and lose much more carbon than they take up

Carbon loss is highly seasonal and varies by river habitat type:

T = tributaries >100m wide
MF = mainstream floodplain
MC = mainstream channels
S = small streams < 100m wide



Richey et al. 2002

Carbon flux and fish

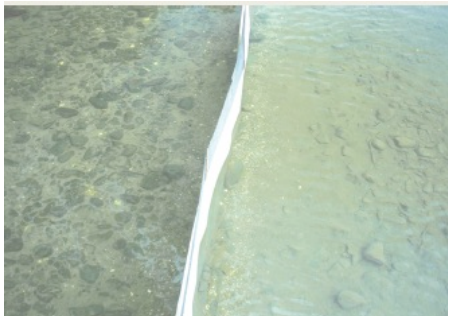
Many Amazon fish, including the flannelmouth characin, feed on detritus and are important players in river carbon transport.

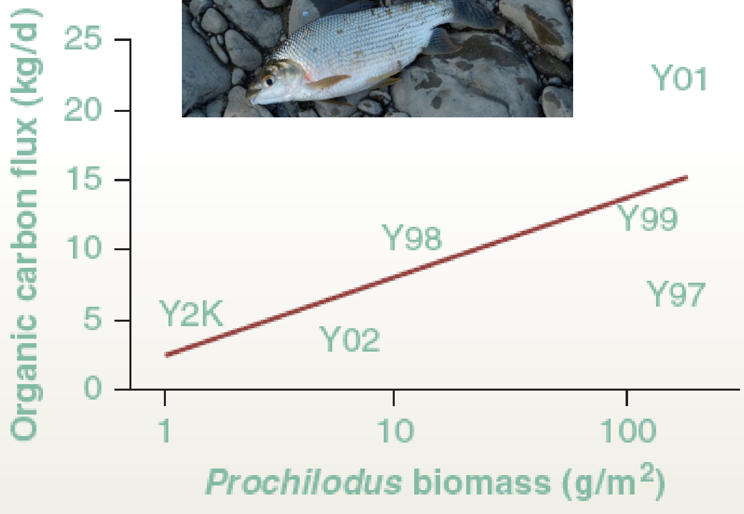
Characins are heavily harvested by local people and are in decline in many areas

An experimental removal of characin with a 210-m plastic divider between control and experimental areas showed that biomass of particulate organic carbon (POC) increased by 450%

Unused POC accumulates and is washed downstream in the flood season

Represents an energy loss to the system





Drought sensitivity in tropical forests

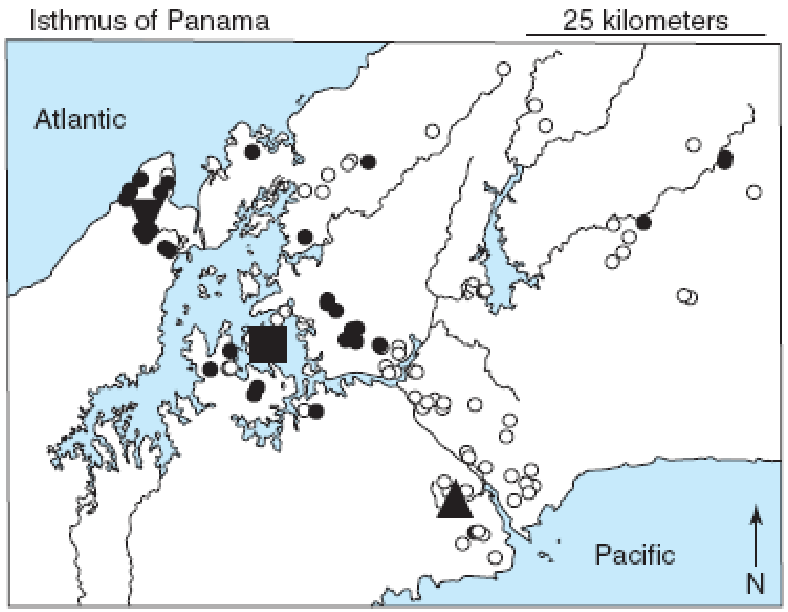
Despite its primary feature being an abundance of moisture, tropical forests experience dry seasons of varying intensity.

- ENSO events substantially add to variability
- Long-term historical droughts also occur

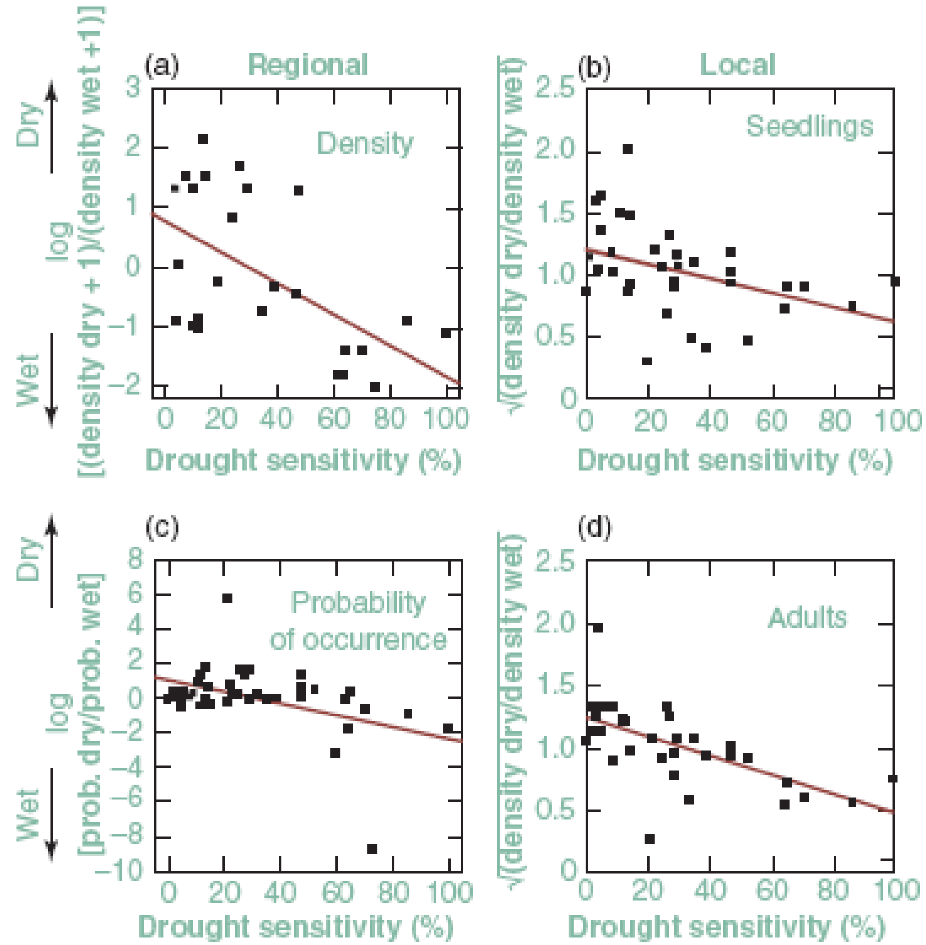
How sensitive are tropical forests to droughts? How could climate change and increasing frequency of ENSO events affect tropical communities?

Drought sensitivity in tropical forests

Study on 48 tree and shrub species across 122 sites in Panama showed strong variation in drought sensitivity



Transplanted seedlings to assess difference in survival under dry and wet conditions, then compared experimental results to where species occurred on the dry – wet gradient



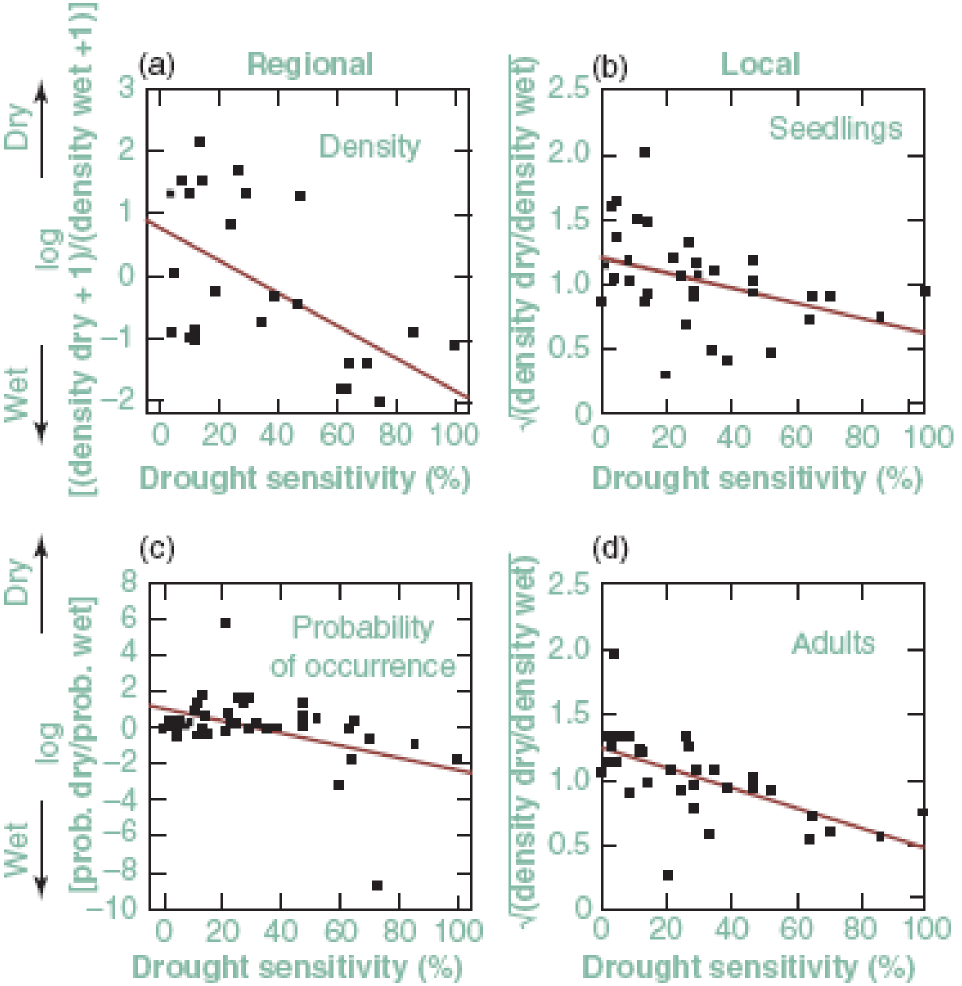
Engelbrecht et al. 2007

Drought sensitivity in tropical forests

Study on 48 tree and shrub species across 122 sites in Panama showed strong variation in drought sensitivity

Drought sensitivity (shown through experimental transplants) was a significant predictor of how relatively common a species was on the dry side of the isthmus

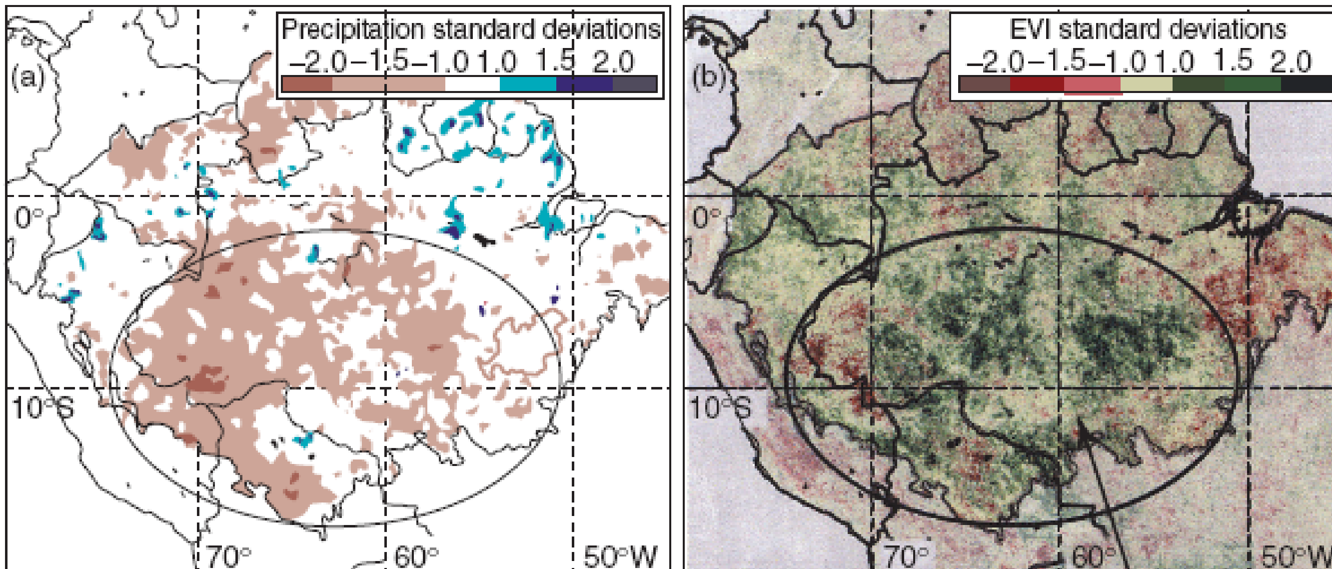
Species more sensitive to drought in experimental conditions were more common on the Atlantic (wet) side of the climatic gradient



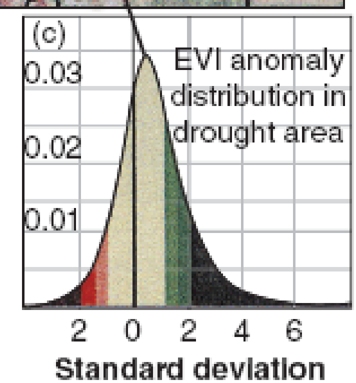
Engelbrecht et al. 2007, *Nature*

Amazonian drought of 2005

A severe and widespread drought occurred in the Amazon in 2005 (July – September) (expected to alter patterns of carbon flux and primary productivity)



Study used Terra satellite’s MODIS data to calculate EVI (enhanced vegetation index). Actually showed *increased greening* during the drought (which was unexpected, but could occur due to decreased cloud cover and increased solar radiation)



Yet, the forest still lost carbon during the drought…

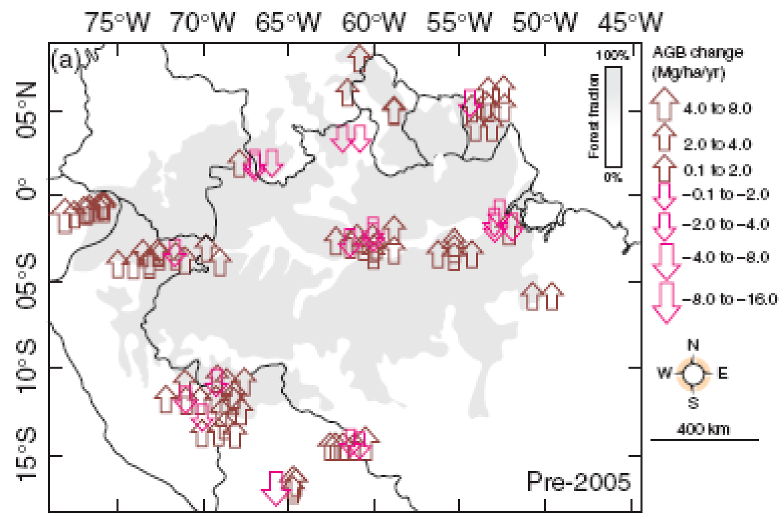
Amazonian drought of 2005

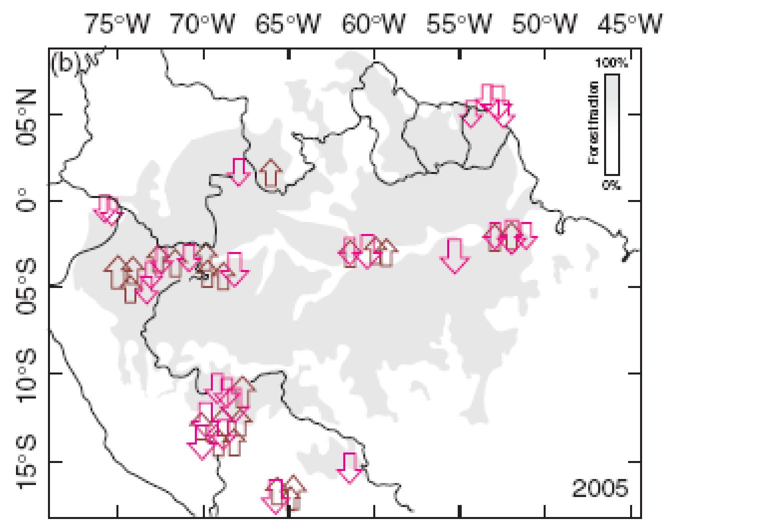
A severe and widespread drought occurred in the Amazon in 2005 (July – September) (expected to alter patterns of carbon flux and primary productivity)

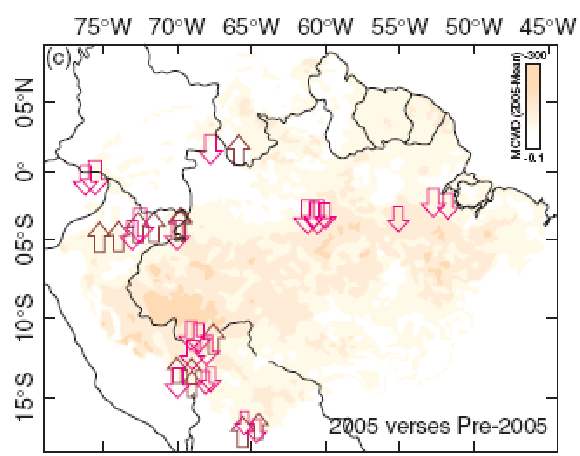
The 2005 drought reversed a multidecadal biomass carbon sink across Amazonia

Prior to 2005, 55 plots showed increase in biomass (0.89 Mg/ha/yr) including throughout several ENSO years – they were operating as carbon sinks

In 2005, there was an overall loss in biomass (-0.71 Mg/ha/yr), more severe in plots with greatest water deficits, and highest mortality







Phillips et al. 2009, *Science*

Sensitivity of tropical forests: too much rain??

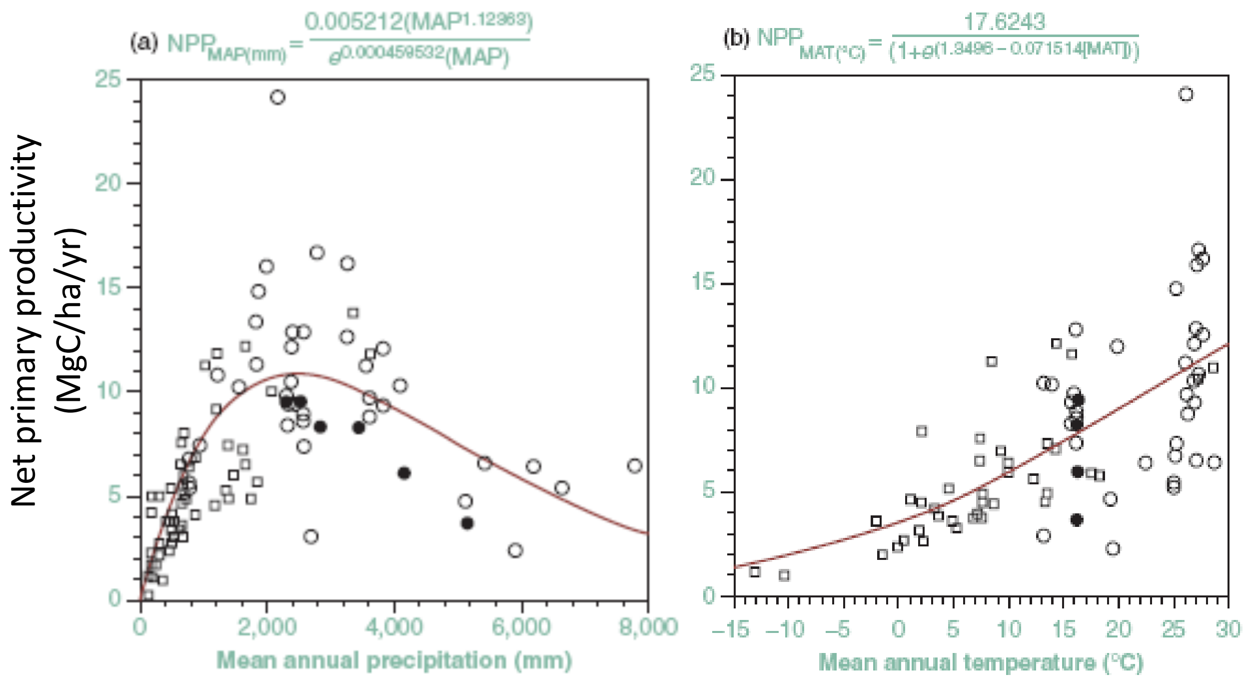
At one end of the spectrum, drought can affect levels of NPP, but so can excess precipitation

Studies from a climate gradient in Maui, Hawaii, showed that as mean annual temp increased, so did productivity, but as precipitation increased, productivity peaked and then declined

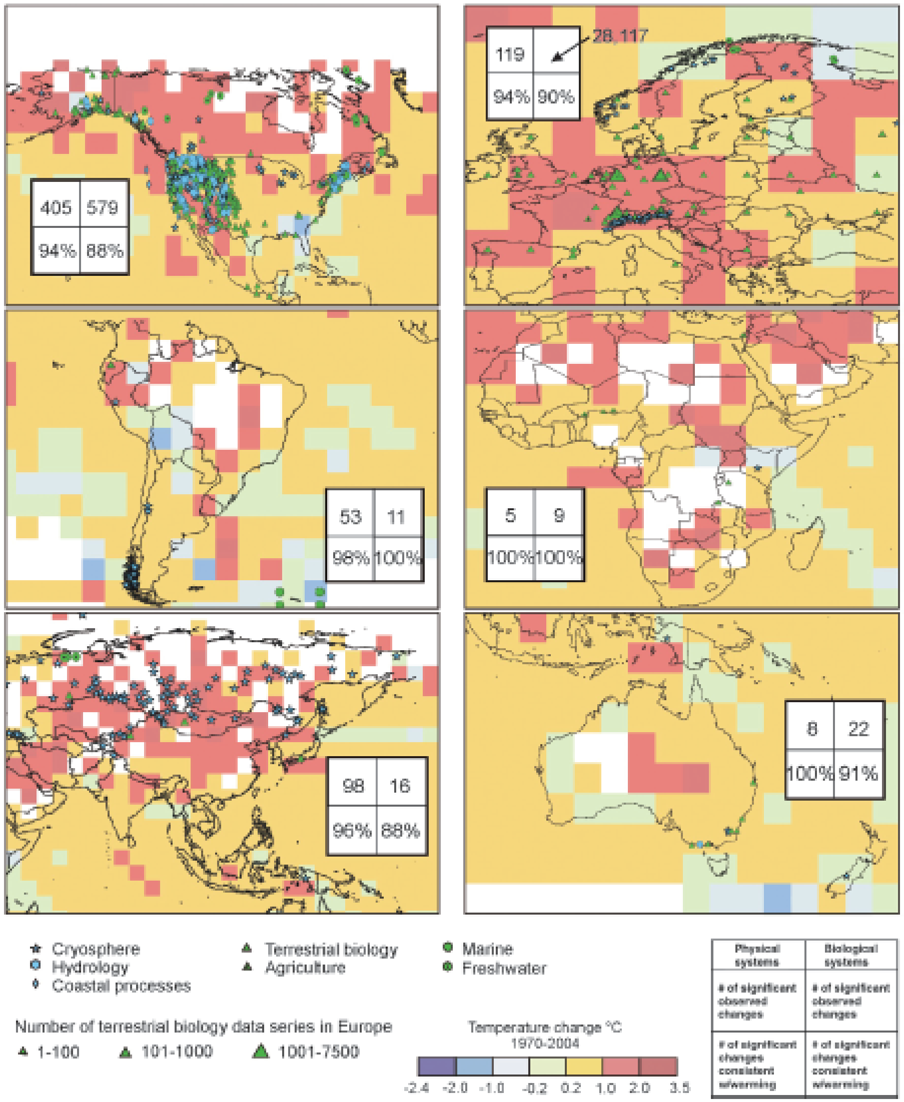
Possible reasons?

Increases in precipitation could be associated with reduced solar radiation

Could result in increased leaching of nutrients (reducing the efficiency of nutrient cycling)



Rising temperature affects on tropical forests



Global temperatures have increased by ~0.6 C in the last century, with the expectation that this trend will continue or intensify

Patterns closely associated with climate change include:

- *Geological changes* in shrinking glaciers, melting permafrost,lake and river warming

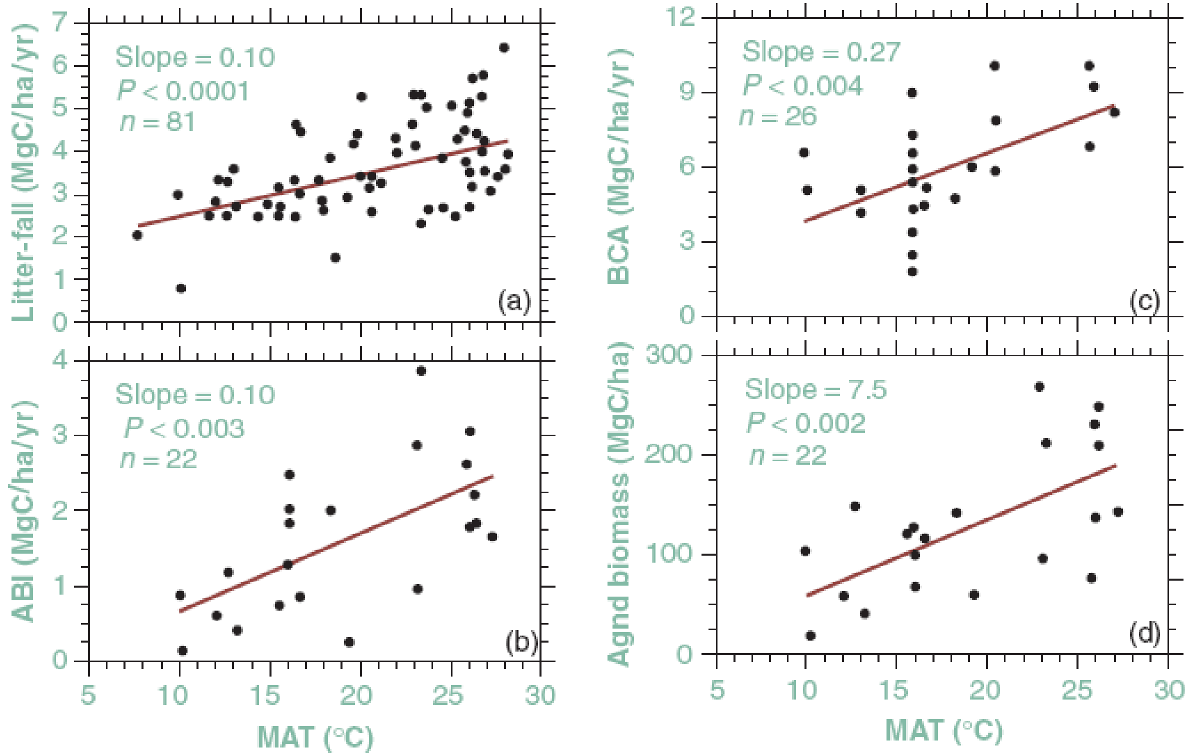
- *Biological changes* in leaf-out patterns, blooming dates, migration arrival and reproduction timing, shifts in species distributions

Rising temperature affects on tropical forests

Mean annual temperature (MAT) is also rising in tropical regions

Among many possible effects, a rise in MAT can have various effects on carbon flux:

Increases in above ground litter production and tree biomass



Soil organic carbon decreases, indicating higher decomposer activity (this can compensate for greater carbon added in biomass) – as NPP increases, so does decomposition, which releases carbon. In other words, overall, these figures could offset each other.

BUT! Tropical deforestation may reduce sufficient forest area and prevent significant carbon sequestration. So it remains an open question…

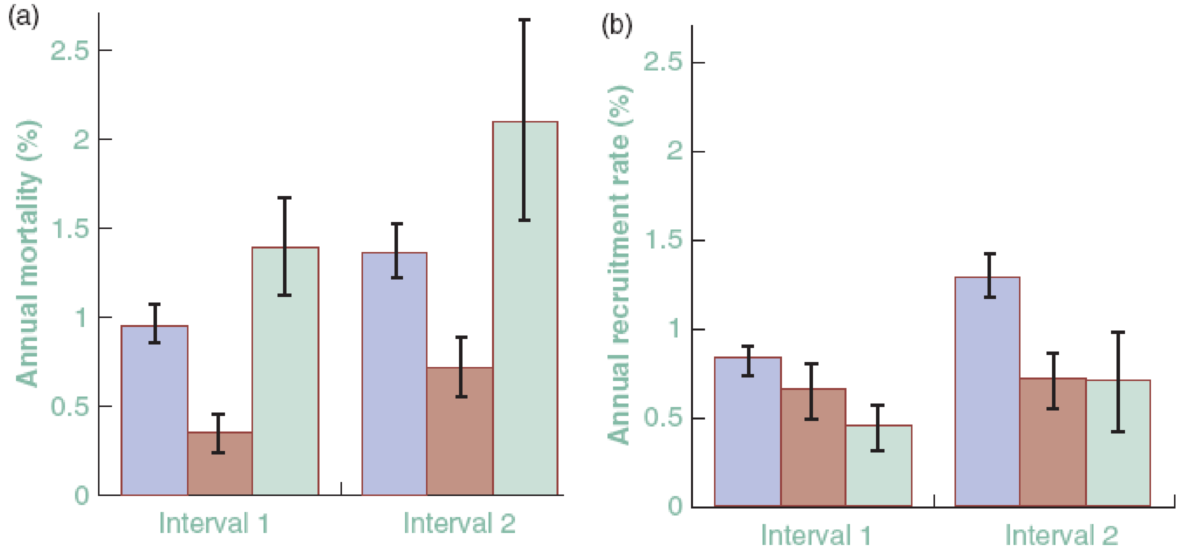
Changes in Amazonian tree communities

A study of permanent 1-hectare tree plots without significant forms of disturbance, showed increases in rates of mortality, and nearly 25% of genera changed in population density or basal area.

Genera of faster-growing species increased in dominance, whereas slower-growing species declined – overall both mortality and recruitment increased

Researchers suggested that rising CO2 was a likely cause for these shifts (other factors like rainfall, ENSO events were constant between intervals)

Shows mortality and recruitment rates across time intervals for:
all trees (blue), and for genera increasing (brown) and decreasing (green) in basal area



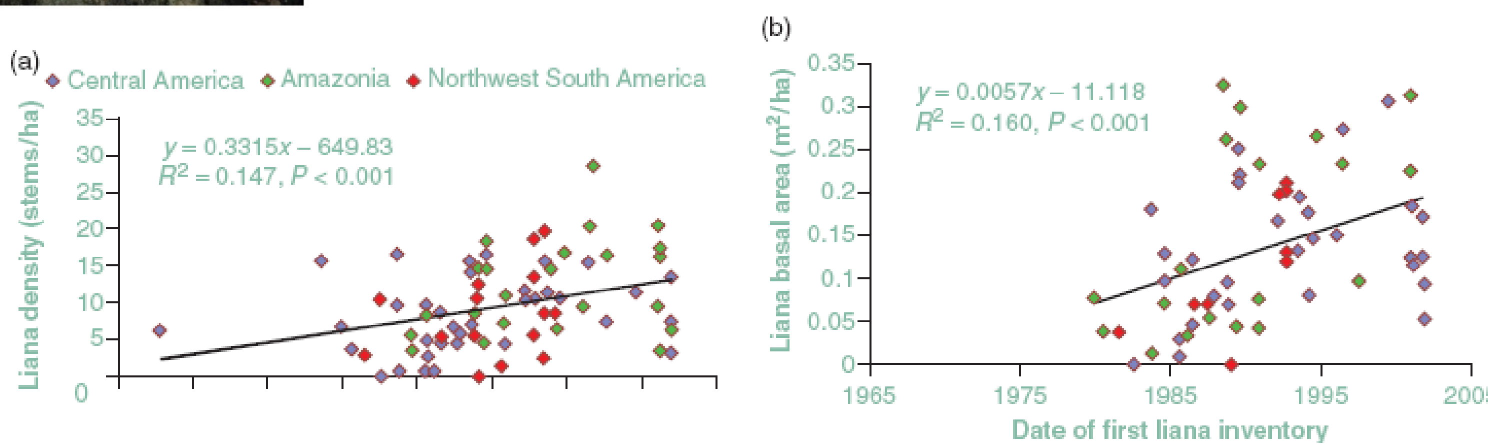
Changes in Amazonian Liana communities

A study across 47 forest interior sites in the Amazon have shown annual increases in liana abundance (stem density and basal area)

Lianas represent ~5% of forest biomass, but up to 40% of leaf productivity

Lianas also respond positively to CO2 fertilization – lianas in deep shade can be stimulated to grow with increases in CO2

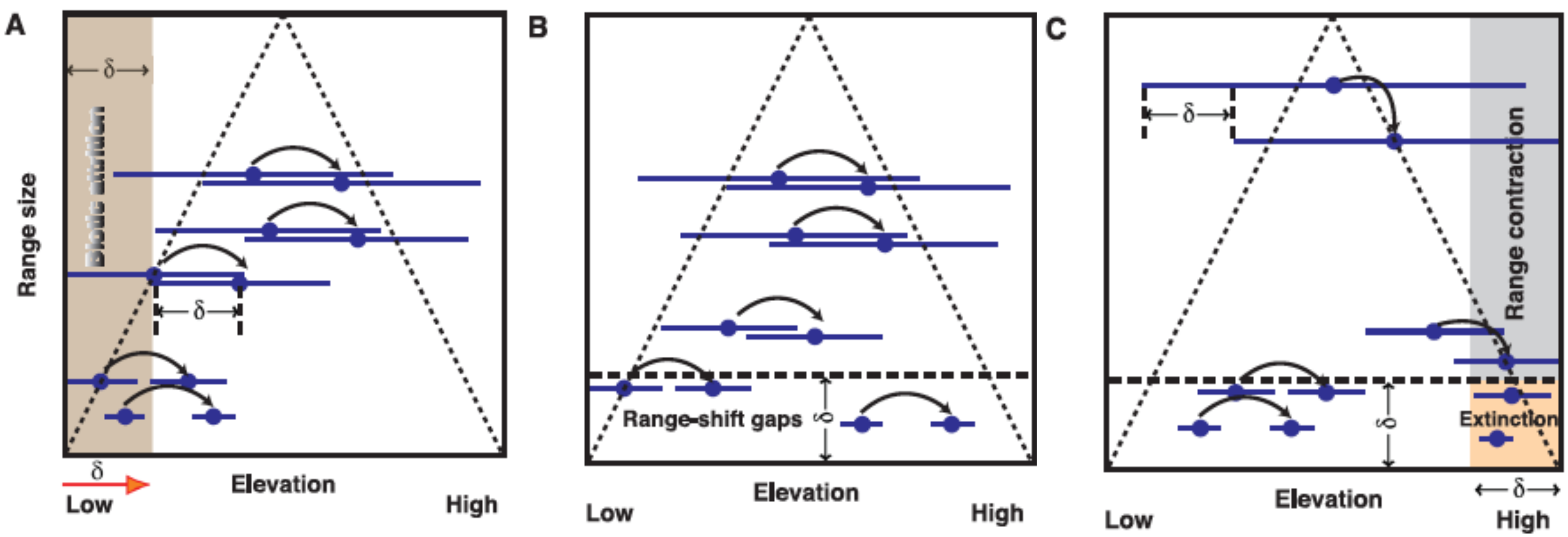
This could affect tree mortality and a shift in forest composition



Lowland biotic attrition and elevational shifts in the tropics

We have observed many range shifts in temperate regions among plants and animals and we expect these range shifts in tropical systems as well – these can ultimately alter community patterns of diversity

Will species found in the areas with highest temperatures (the tropical lowlands) adapt or migrate elsewhere? For species in vast lowland forests, where will they go?

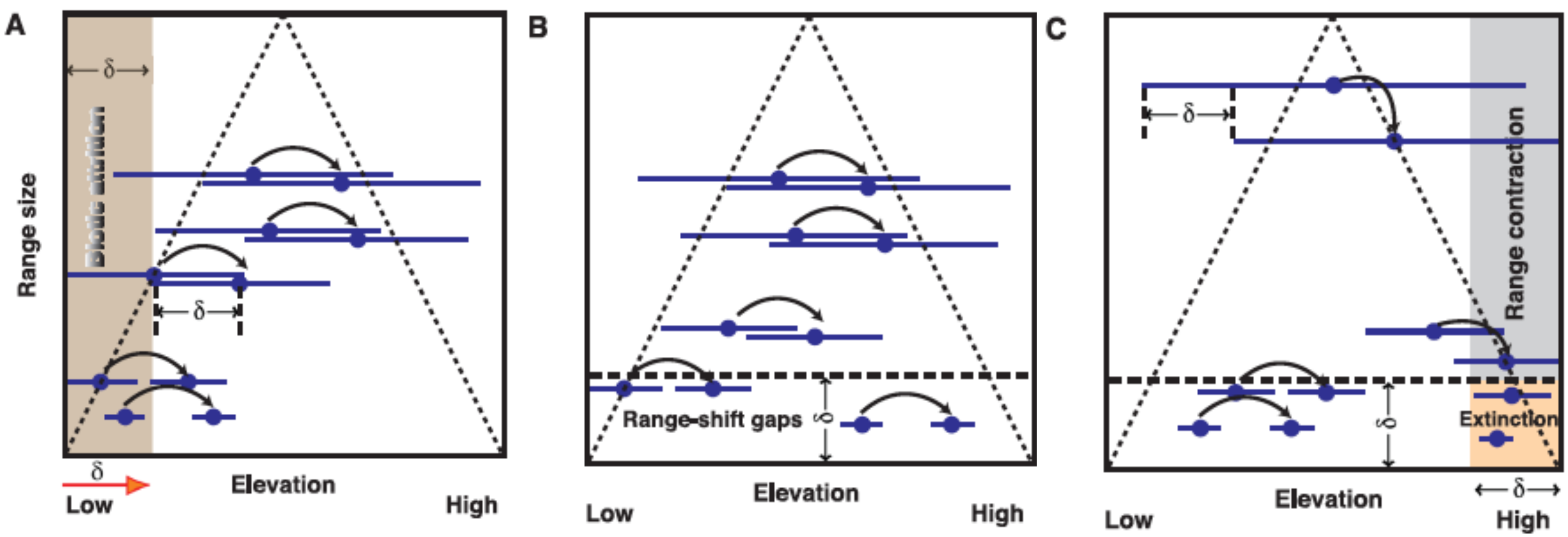


Lowland biotic attrition and elevational shifts in the tropics

If lowland species move elevationally in response to warming temperatures, there is no species pool to replace them, which could result in lowland biotic attrition (an overall loss in species richness)

Some species in close proximity to elevational gradients may move upslope

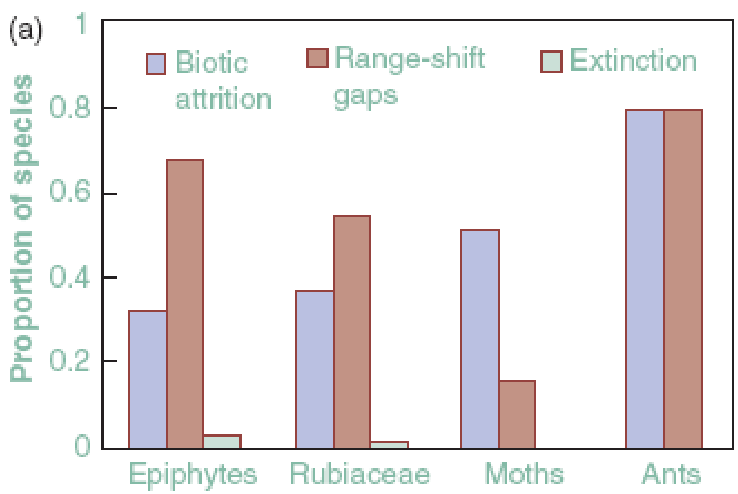
Range shift gaps (gaps between current and projected ranges) and range contractions can also occur

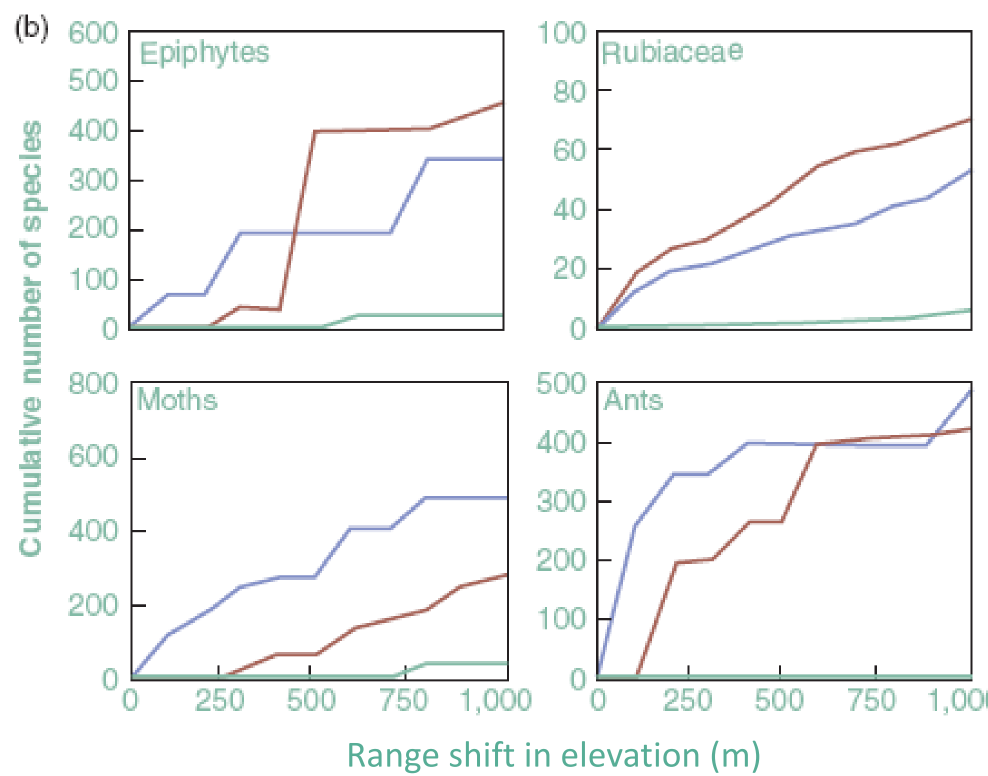


Colwell et al. 2008

Lowland biotic attrition and elevational shifts in the tropics

Using a model assuming a 3.2 C increase in temperature over the next century, and a 600-m shift upslope, 53% of species would be subject to biotic attrition and 51% would experience range-shift gaps, and some would experience mountaintop extinctions





Proportion of species in the lowlands subject to decline through biotic attrition or faced with range-shift gaps

More species will face these challenges as the extent of range shift increases

Colwell et al. 2008

Carbon sink or source?

Clearly this is not a simple question, and the answer is far from certain

- Tree species loss with climate change, and the effect of losses on carbon storage will depend on the species; extinction of species with high wood density could result in more severe declines in carbon storage
- Increased liana abundance could result in decreases in overall carbon storage
- Rising temperatures, more severe and frequent droughts, anthropogenic effects may collectively make tropical forests carbon sources