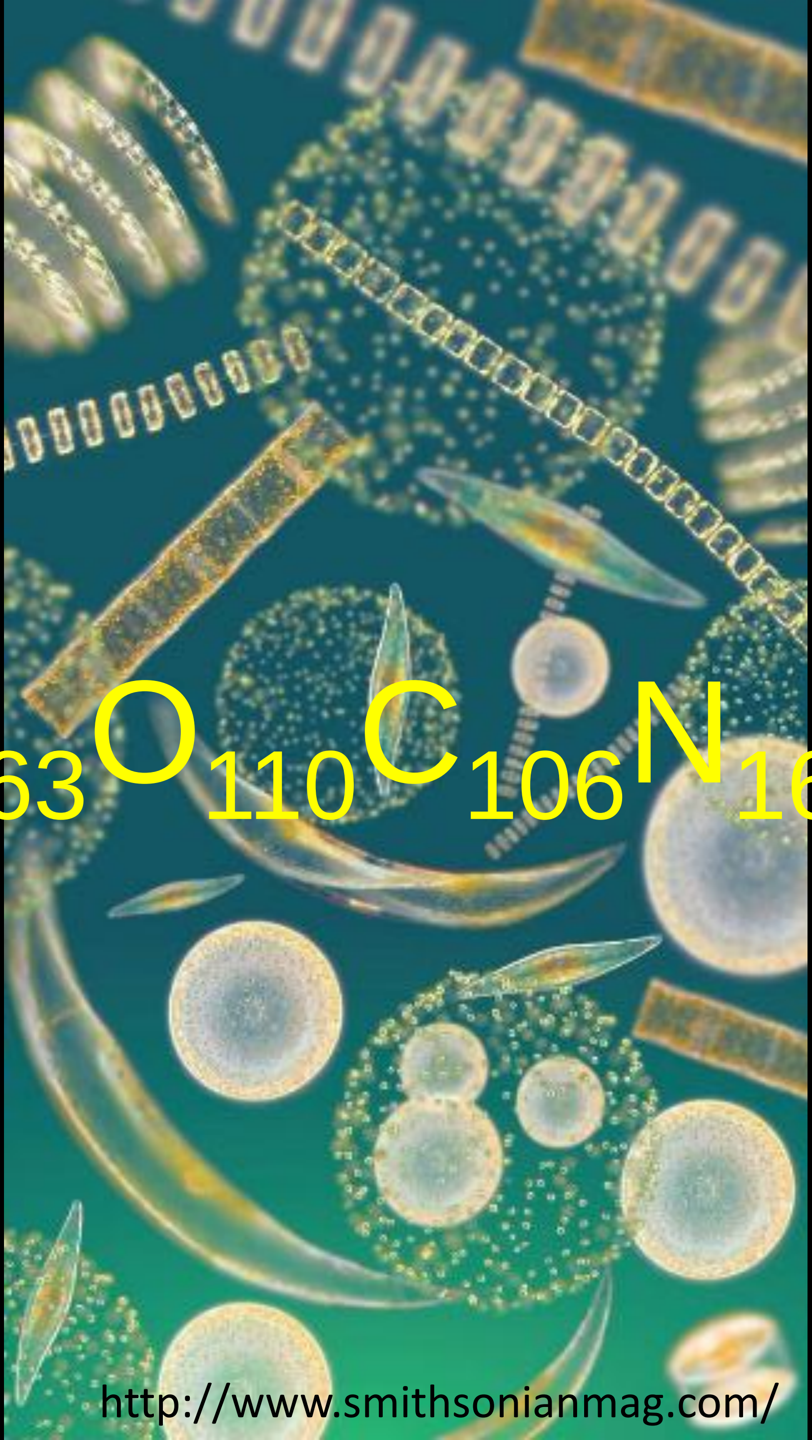
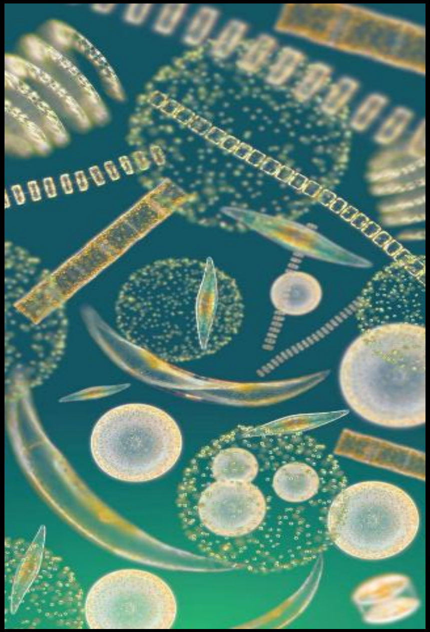
$H_{375}O_{132}C_{88}N_{6}Ca_{1}P_{1}$



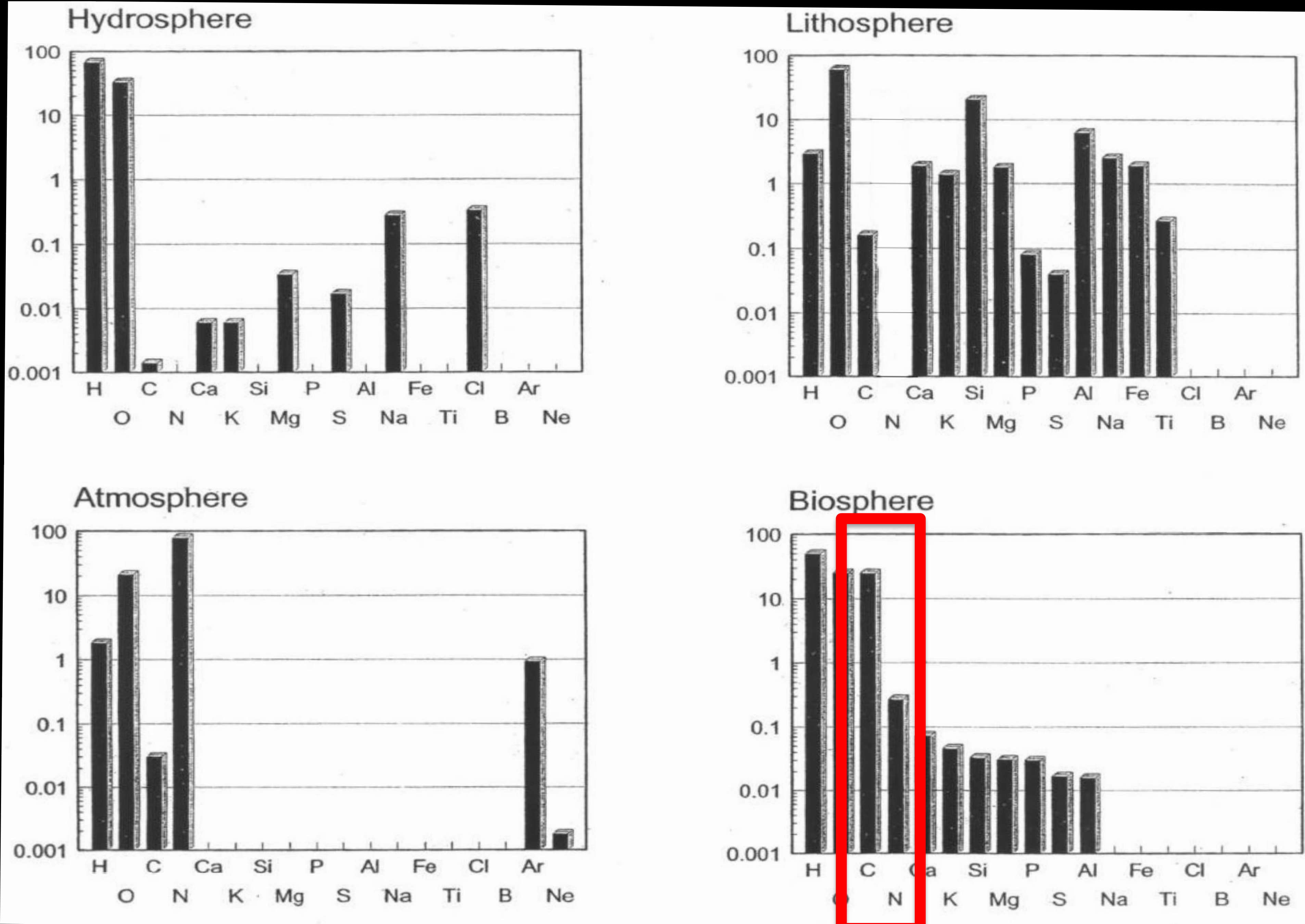
$H_{263}O_{110}C_{106}N_{16}P_{1}$

http://www.smithsonianmag.com/

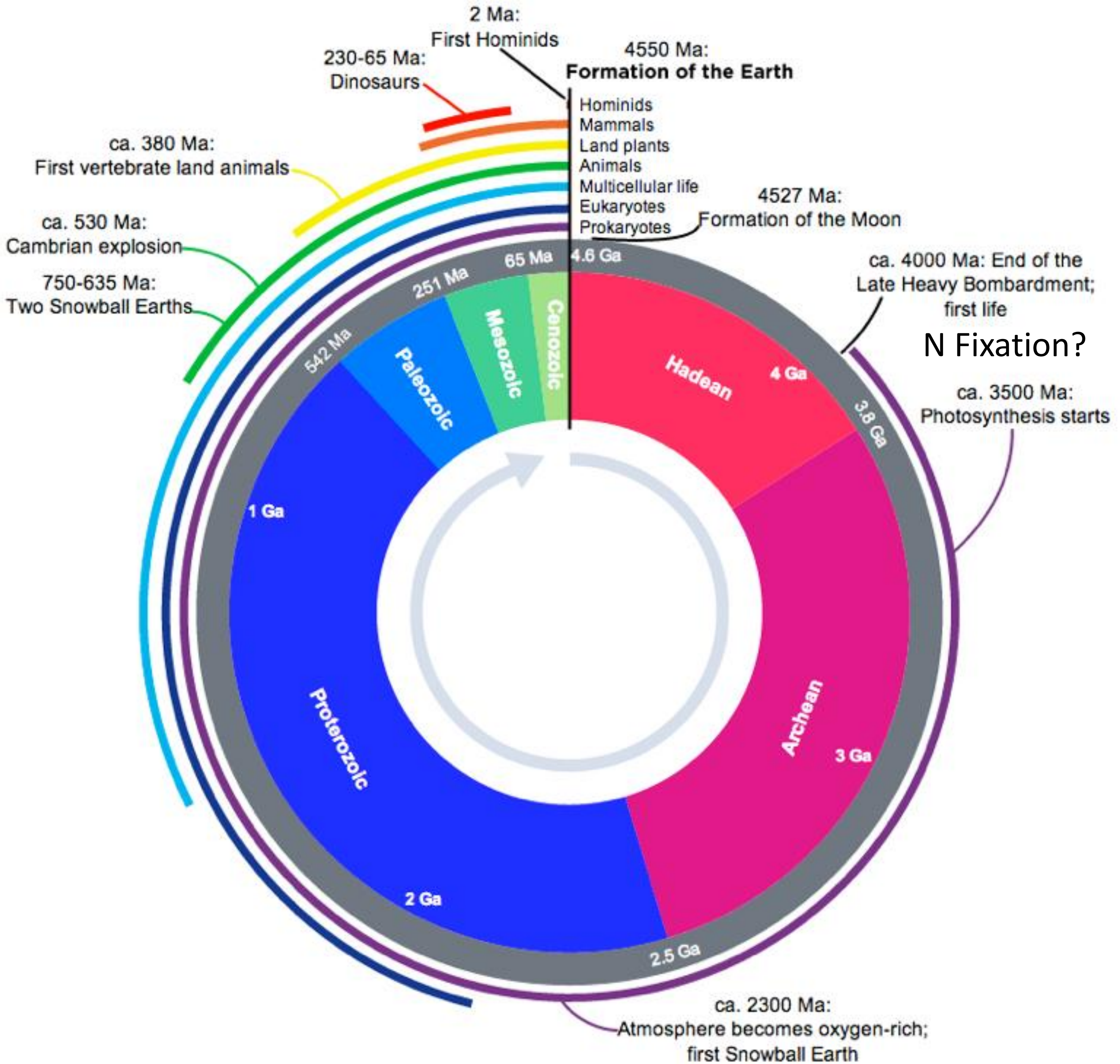
$H_{263}O_{110}C_{106}N_{16}P_{1}$



$H_{375}O_{132}C_{88}N_{6}Ca_{1}P_{1}$



Hydrosphere
100
10
1
0.1
0.01
0.001
H C Ca Si P Al Fe Cl Ar
O N K Mg S Na Ti B Ne
Lithosphere
100
10
1
0.1
0.01
0.001
H C Ca Si P Al Fe Cl Ar
O N K Mg S Na Ti B Ne
Atmosphere
100
10
1
0.1
0.01
0.001
H C Ca Si P Al Fe Cl Ar
O N K Mg S Na Ti B Ne
Biosphere
100
10
1
0.1
0.01
0.001
H C Si P Al Fe Cl Ar
N K Mg S Na Ti B Ne


2 Ma:
First Hominids
4550 Ma:
Formation of the Earth
230-65 Ma:
Dinosaurs
Hominids
Mammals
Land plants
Animals
Multicellular life
Eukaryotes
Prokaryotes
ca. 380 Ma:
First vertebrate land animals
4527 Ma:
Formation of the Moon
ca. 530 Ma:
Cambrian explosion
750-635 Ma:
Two Snowball Earths
ca. 4000 Ma: End of the
Late Heavy Bombardment;
first life
N Fixation?
ca. 3500 Ma:
Photosynthesis starts
65 Ma
4.6 Ga
251 Ma
542 Ma
Cenozoic
Mesozoic
Paleozoic
Hadean
4 Ga
3.8 Ga
1 Ga
Proterozoic
Archean
3 Ga
2 Ga
2.5 Ga
ca. 2300 Ma:
Atmosphere becomes oxygen-rich;
first Snowball Earth

Biological Nitrogen Fixation

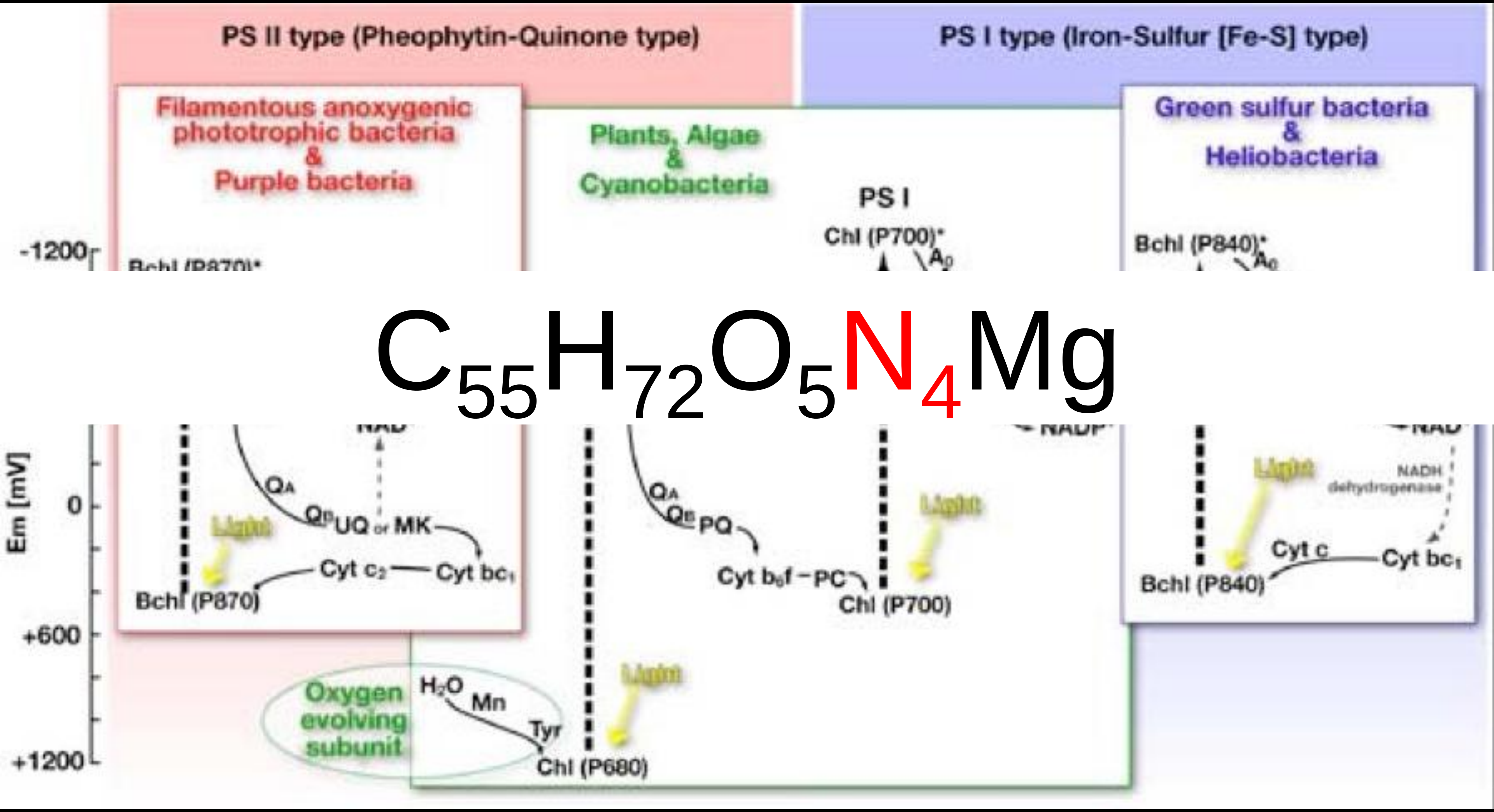
Evolved ≈3.5 billion years ago

Converts N_2 into NH_3

Energetically expensive
(16ATP for 1 N)

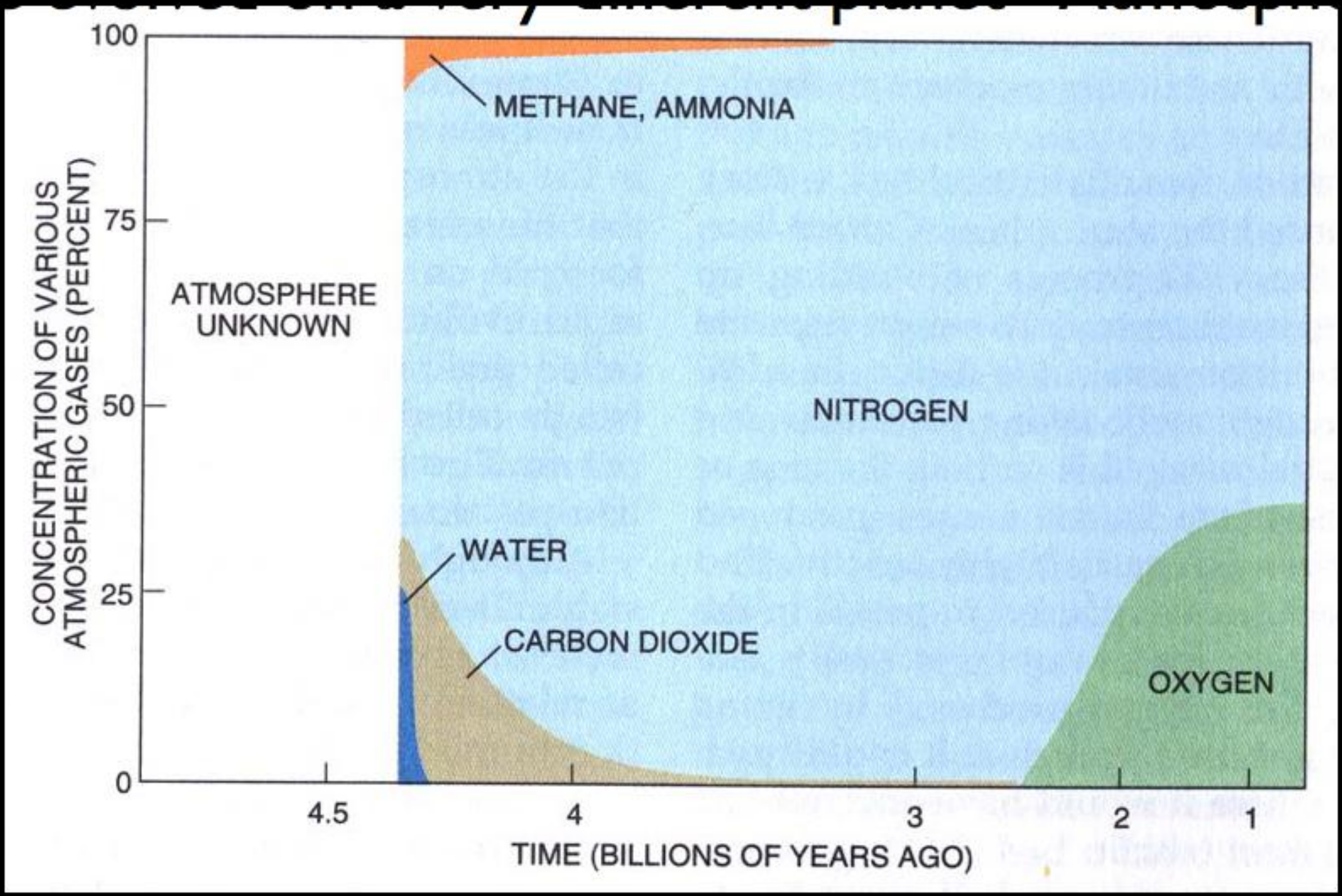
Poisoned by oxygen

Photosynthesis requires nitrogen



$$C_{55}H_{72}O_5N_4Mg$$

Oxygenic photosynthesis and N fixation evolve in an anoxic world, but are so important that they remain basically unchanged for 3 billion years.



Today photosynthesis and other key processes are limited by nitrogen

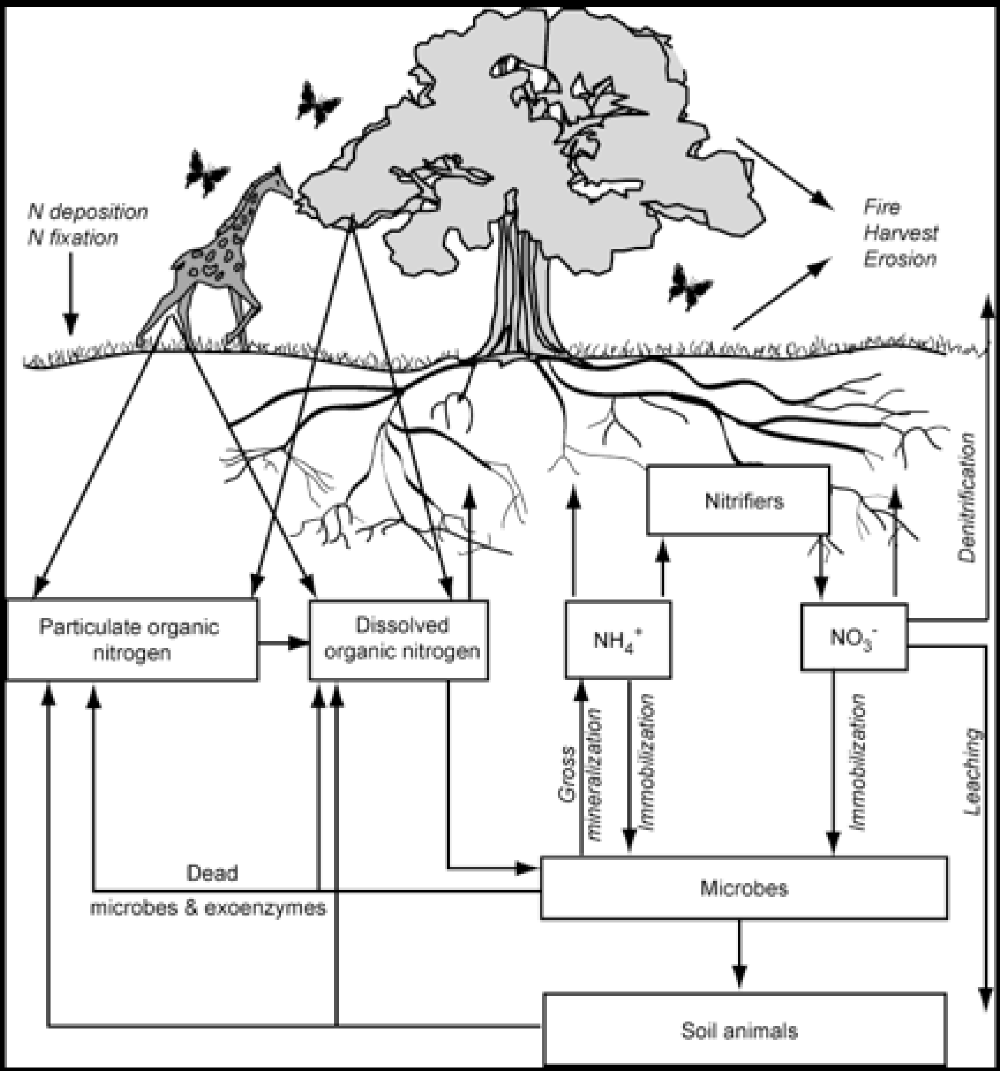
Nitrogen limitation on land and in the sea: How can it occur?

PETER M. VITOUSEK[1] & ROBERT W. HOWARTH[2]

[1] *Department of biological Sciences, Stanford University, Stanford, CA 94305, USA*

[2] *Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853, USA*

Nitrogen Cycle Basics



Transformations mediated by microbes (auto and heterotrophic)

Inputs via fixation + deposition

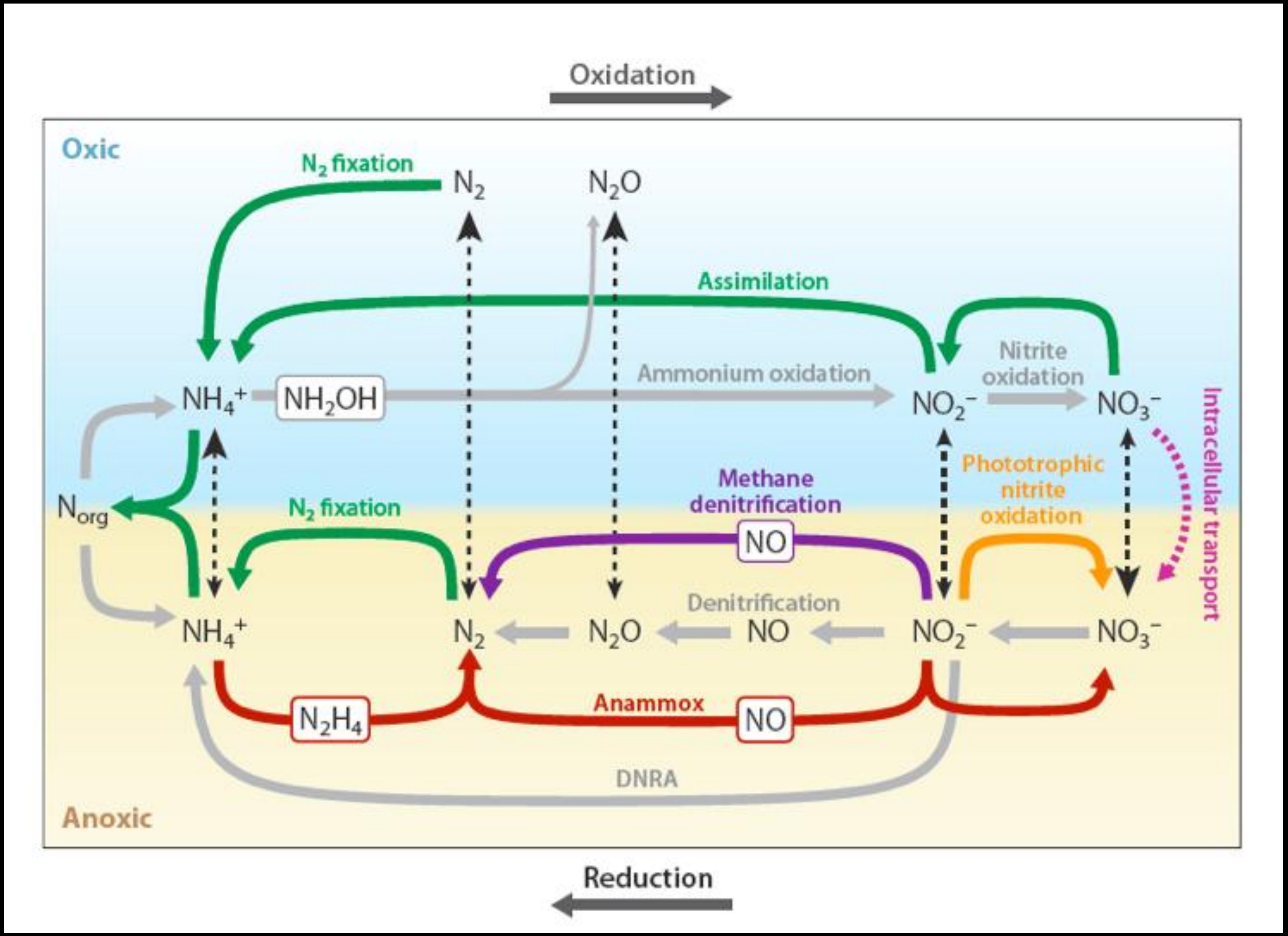
Outputs via leaching and gas losses (denitrification) +

Mineral forms used by plants (NO_3^- and NH_4^+) + little DON

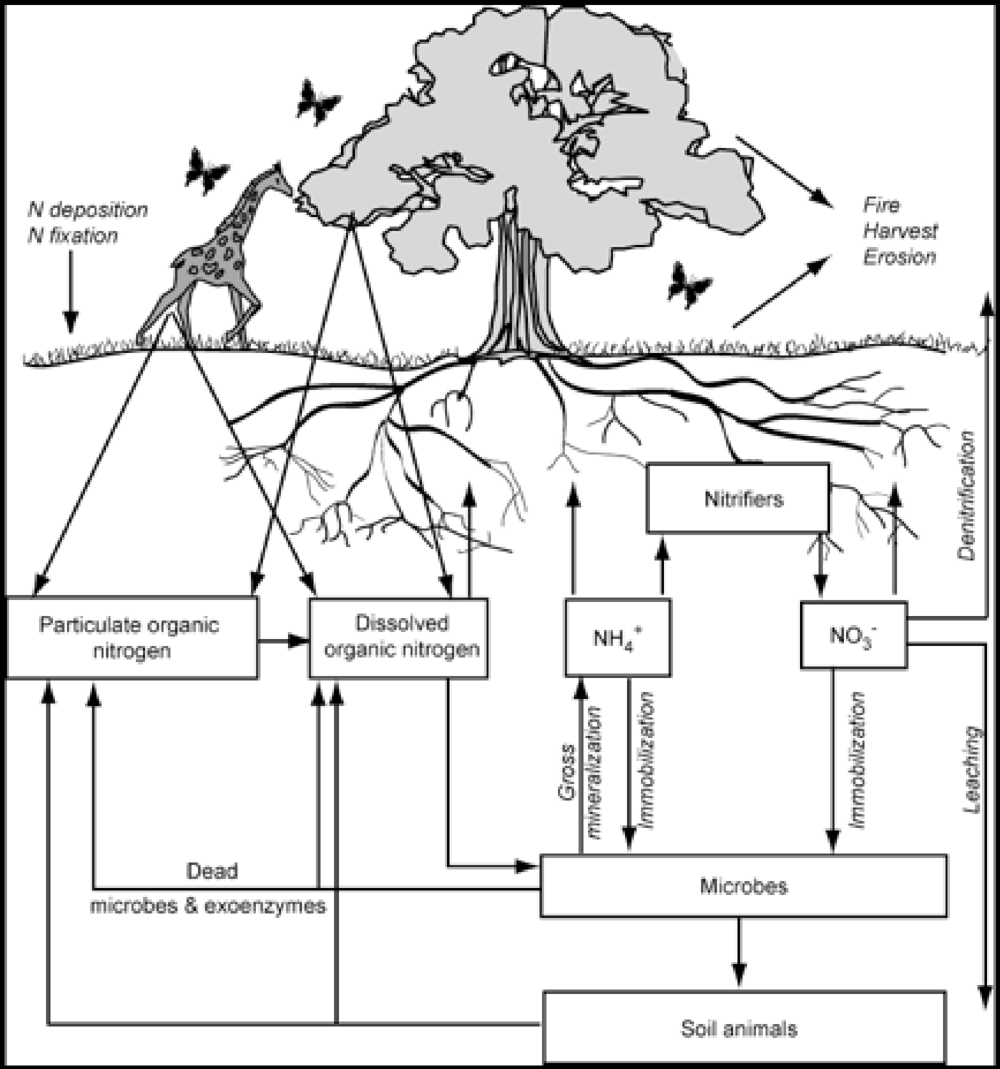
Losses of nitrate discriminate against ^{15}N, leaving it behind.

The N cycle, like life, is a redox driven process.

The N Cycle is Driven by Redox



Ecosystem Mass Balance

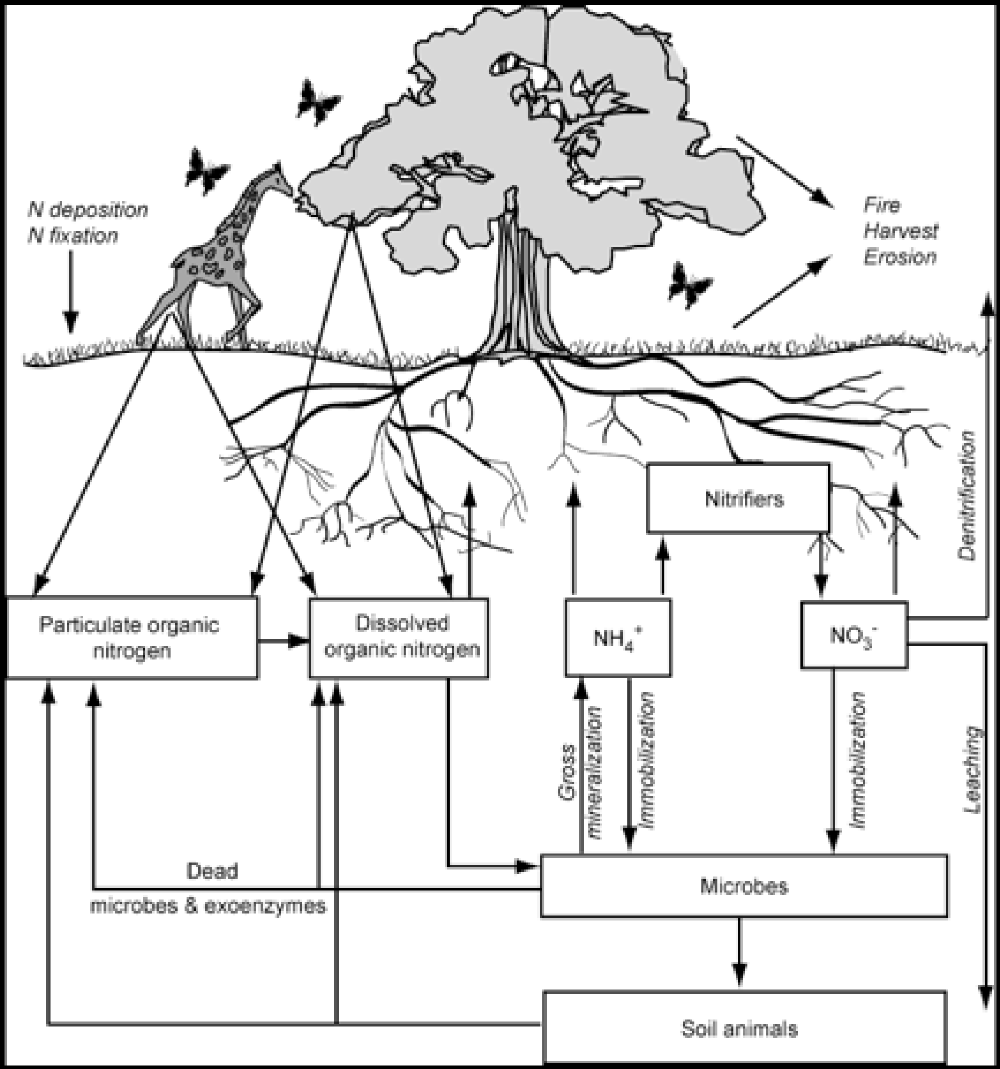


IF Inputs > Outputs

THEN N pools grow

Losses grow

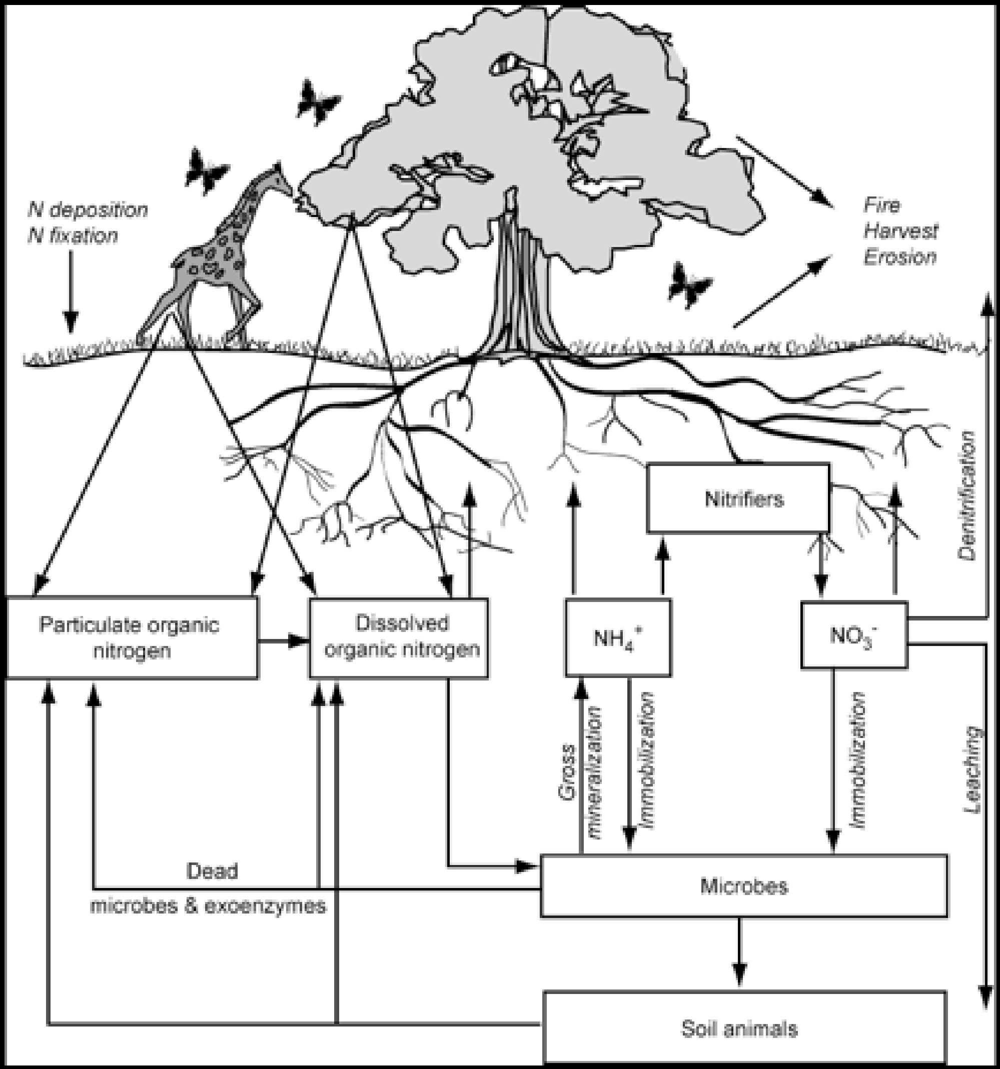
Ecosystem Mass Balance



IF Inputs > Outputs
THEN N pools grow
Losses grow

IF Outputs > Inputs
THEN N pools shrink
Losses shrink

Ecosystem Mass Balance

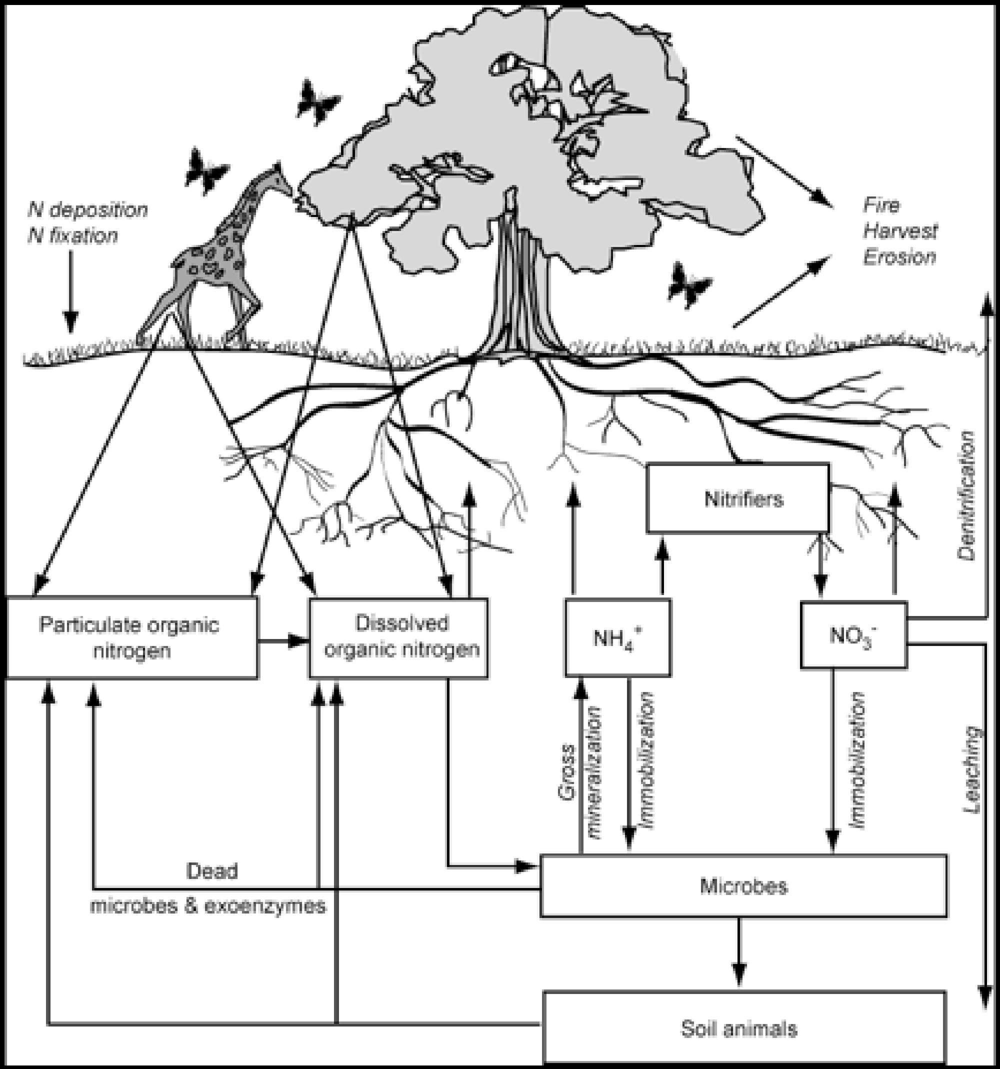


IF Inputs > Outputs
THEN N pools grow
Losses grow

IF Outputs > Inputs
THEN N pools shrink
Losses shrink

IF N availability > demand
THEN Available N losses high

Ecosystem Mass Balance



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IF N availability < demand
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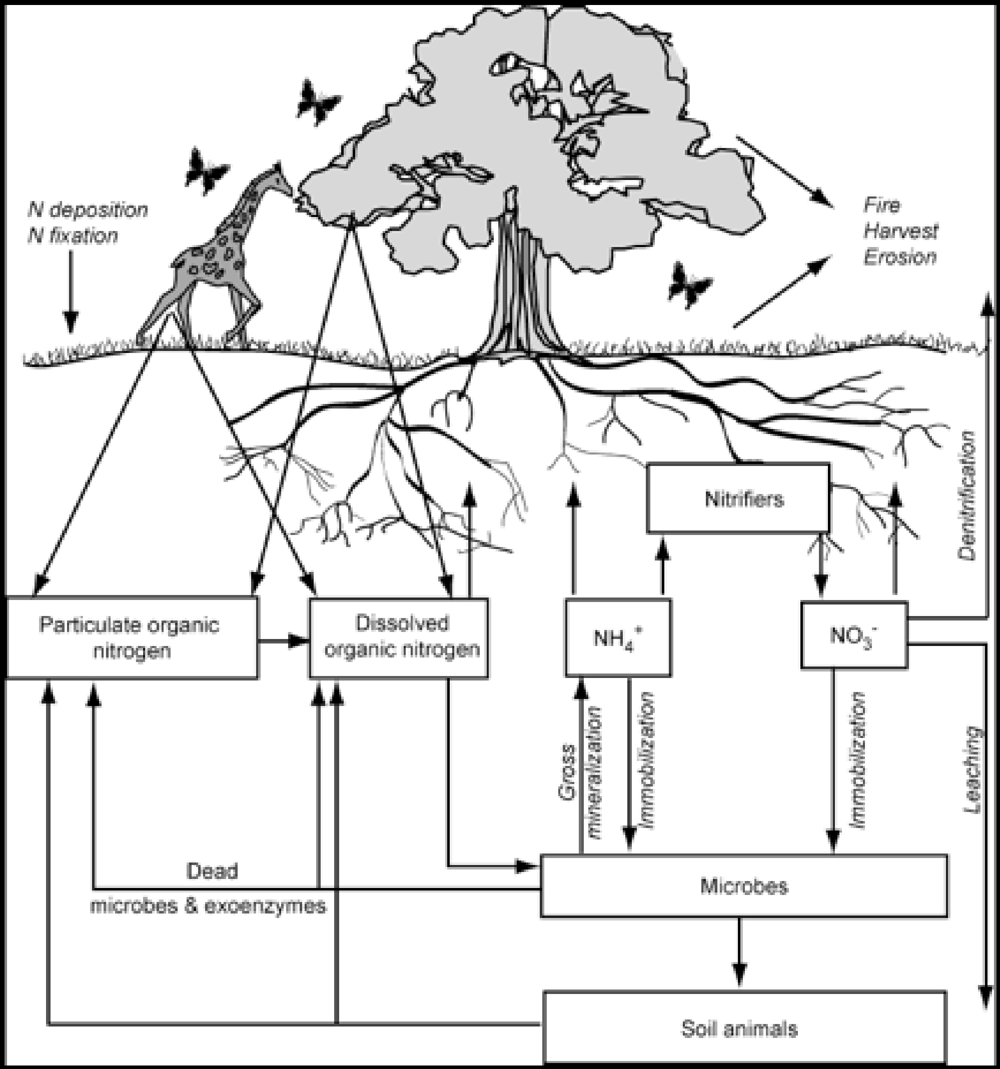
Ecosystem Mass Balance



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Losses shrink

IF N availability > demand
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IF N availability < demand
THEN Available N losses low

Global patterns in the N cycle

Fixation highest in tropics

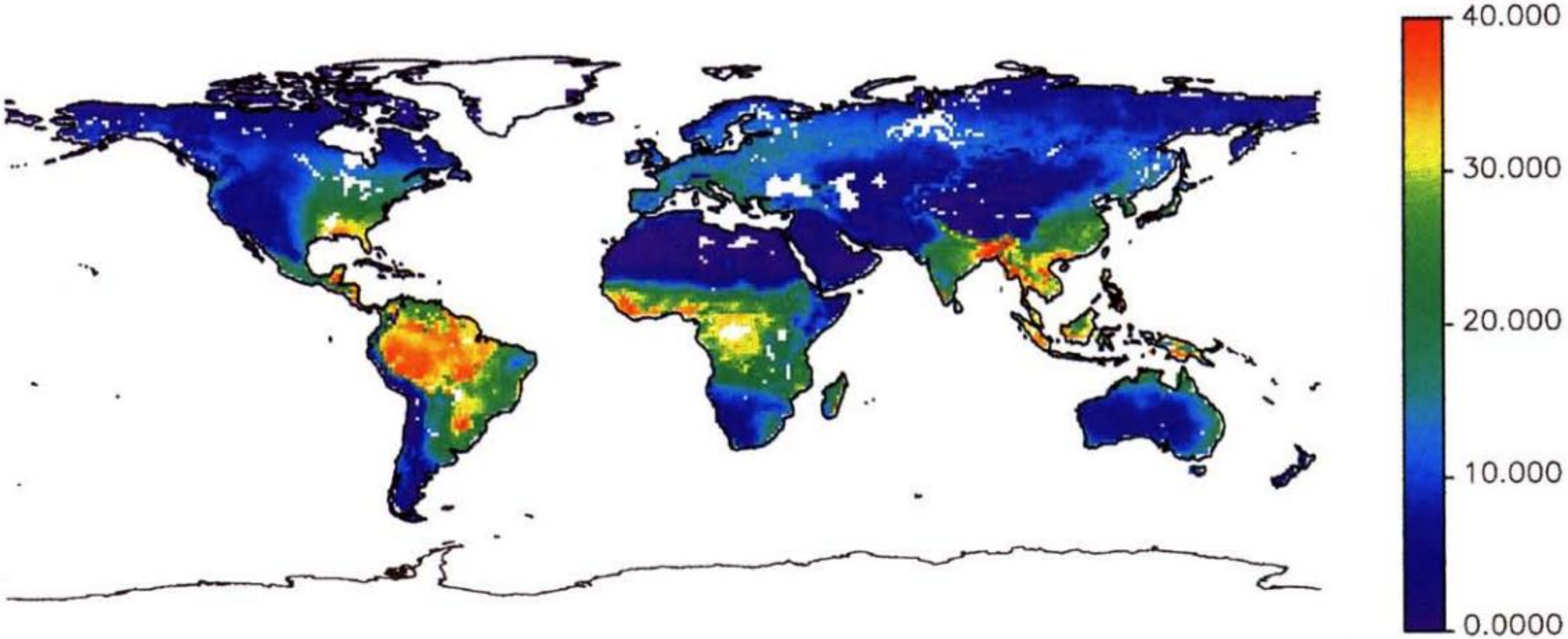


Plate 2. Mapped potential annual BNF by natural ecosystems based on the relationship between the central estimates of BNF (N fixation = 0.234(ET) - 0.172) and ecosystem ET. Values are kg N ha^{-1} yr^{-1}. White areas represent regions where modeled ET values are unavailable.

Cleveland et al., 1999

NUE lower in tropics

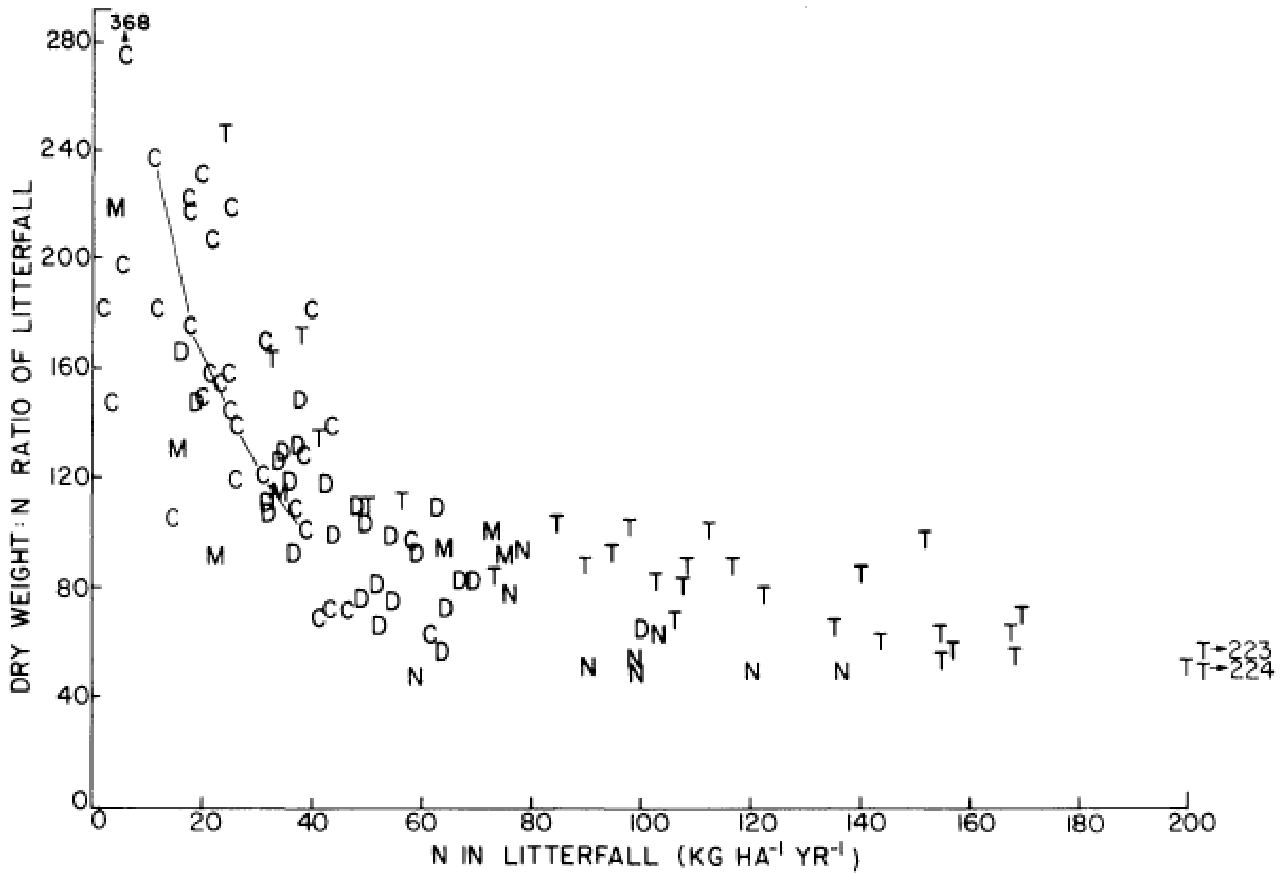
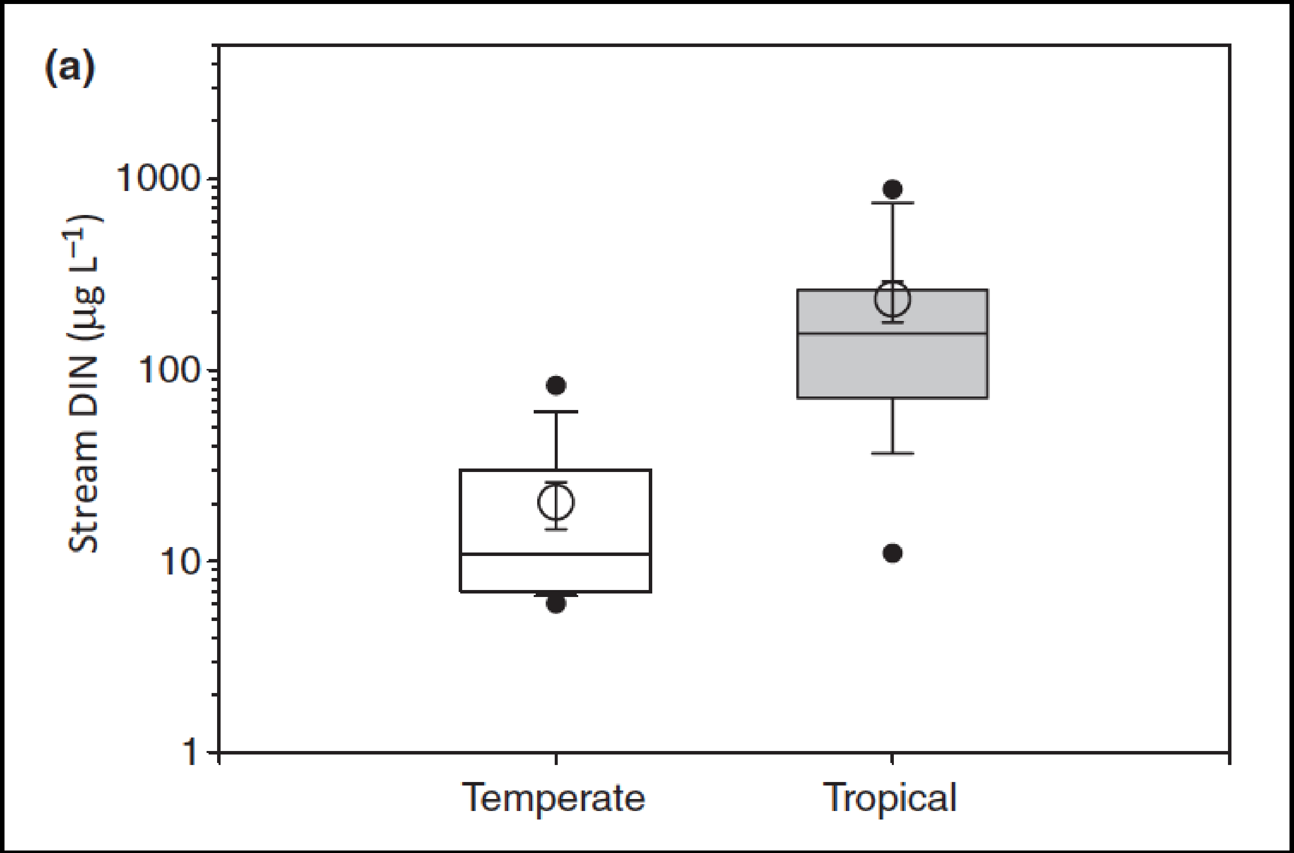


FIG. 4.—The relationship between the amount of nitrogen in fine litterfall and the dry mass to nitrogen ratio of that litterfall. Symbols as in fig. 1.

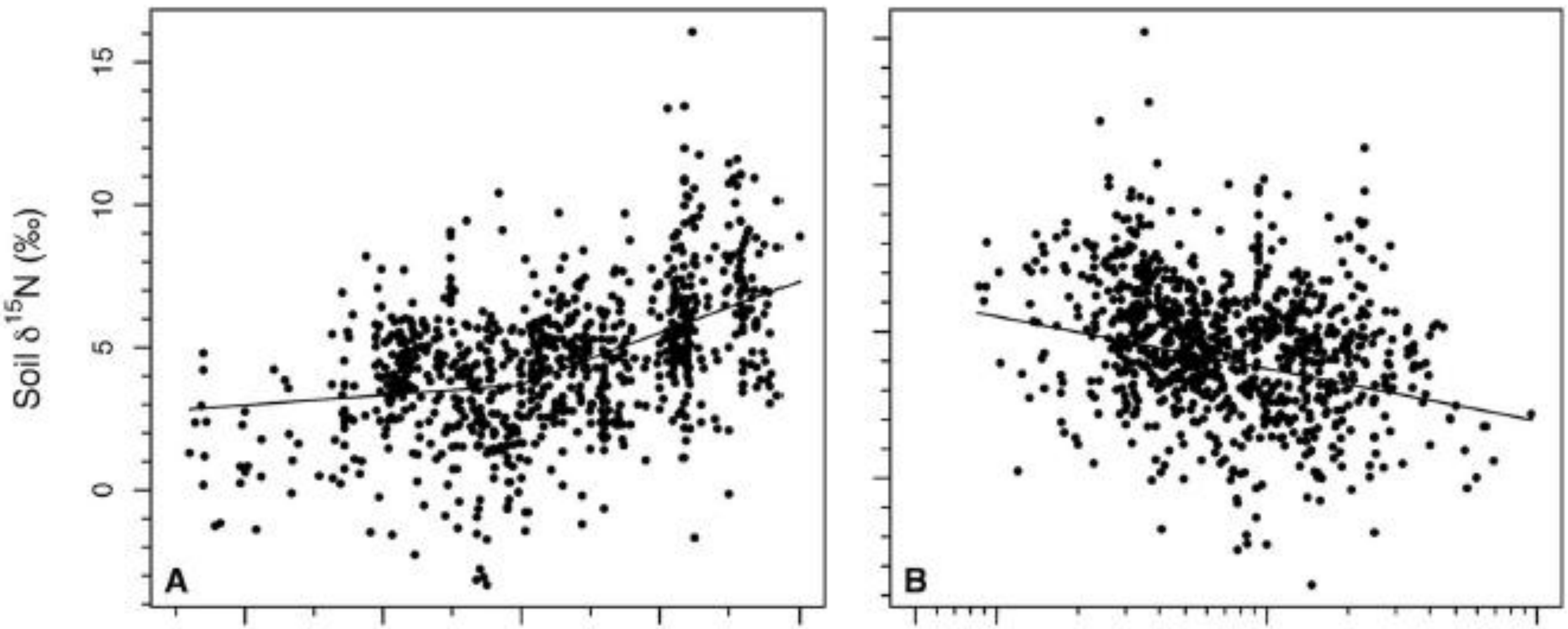
Vitousek 1982

NO_3^- losses higher in tropics



Brookshire et al 2012

Soil $\delta^{15}N$ higher in tropics



-10 0 10 20 30

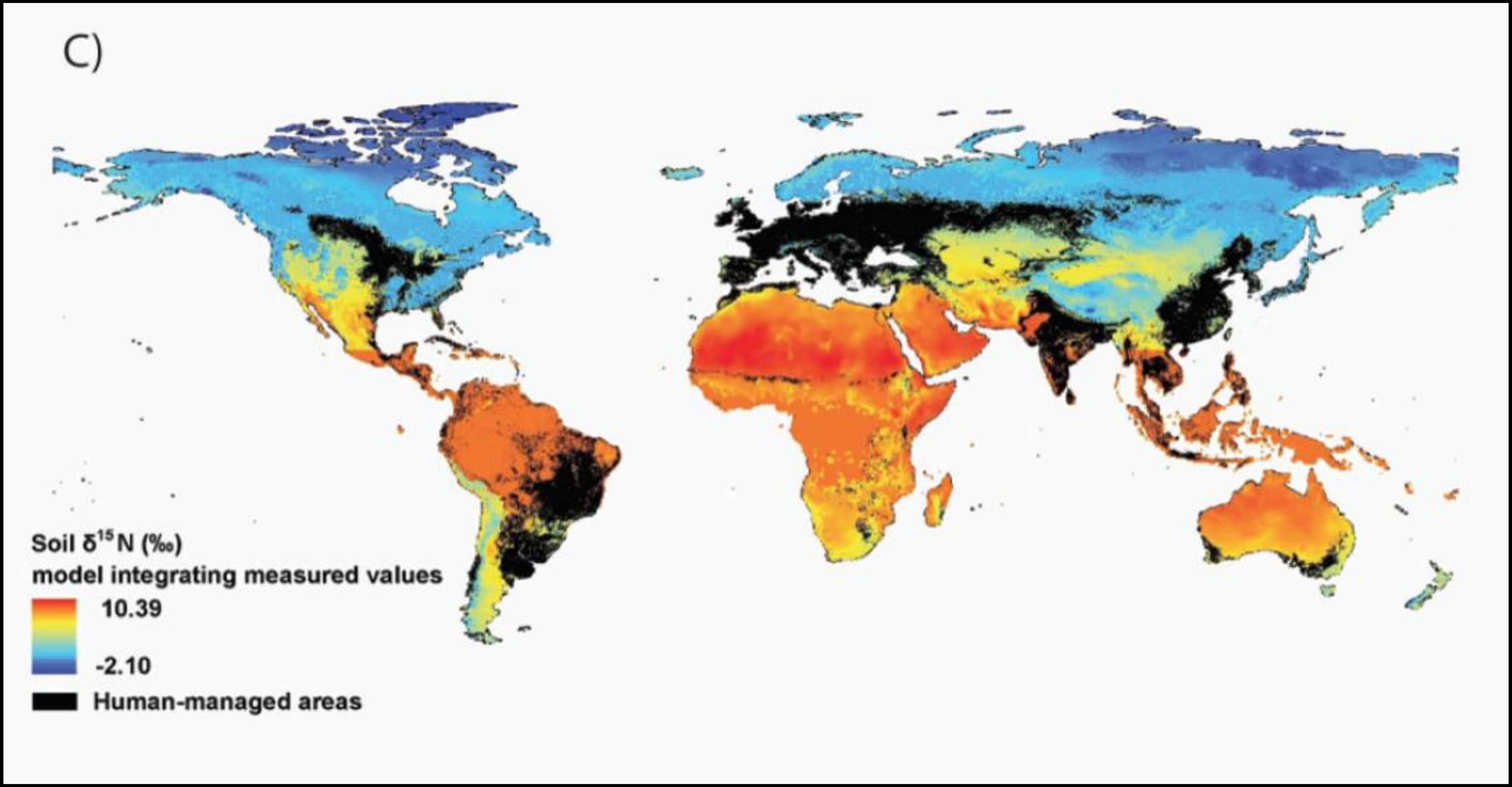
MAT (°C)

100 1,000 10,000

MAP (mm/yr)

Craine et al., 2015

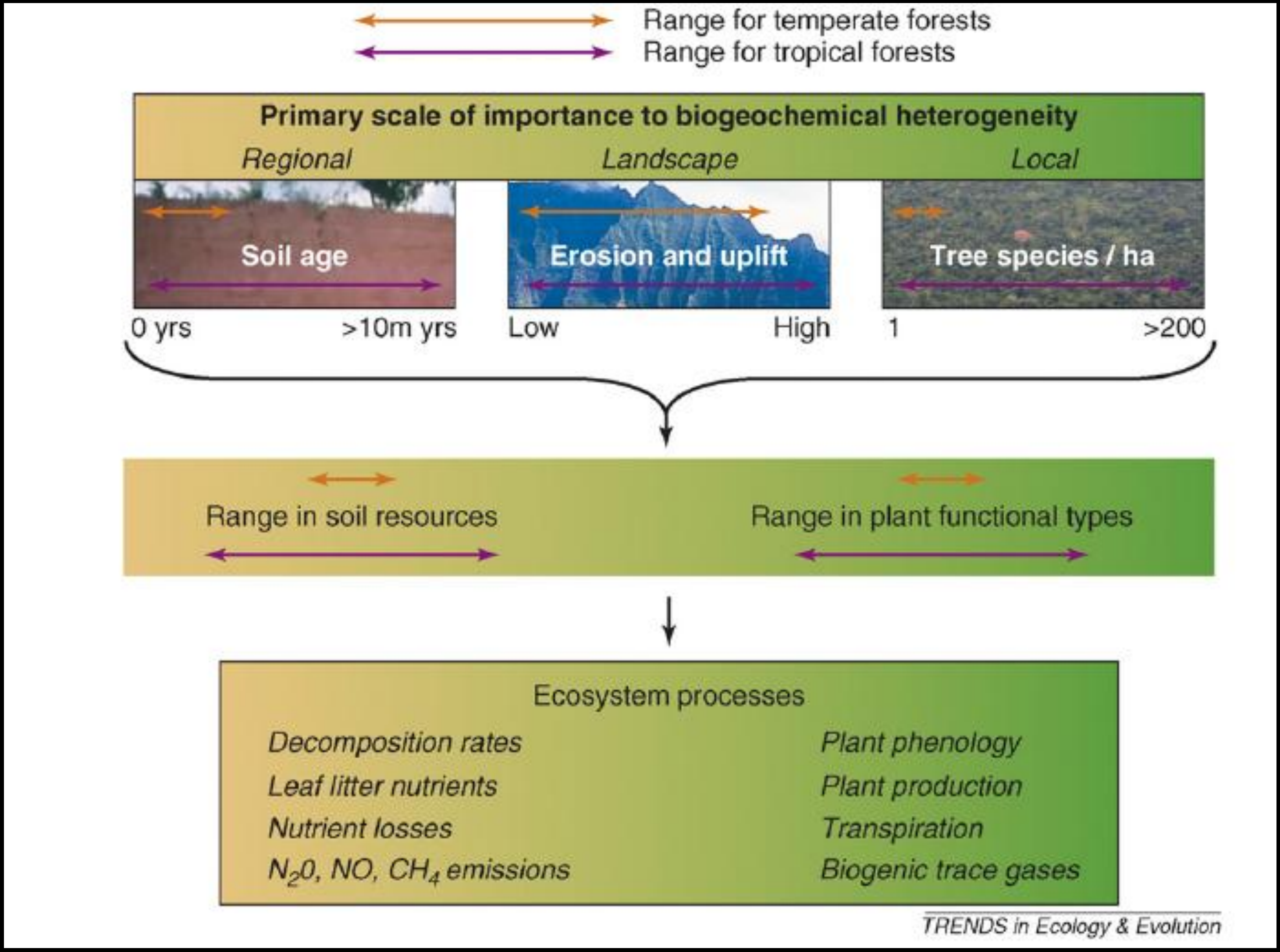
Soil $\delta^{15}N$ higher in tropics



Houlton and Bai 2009

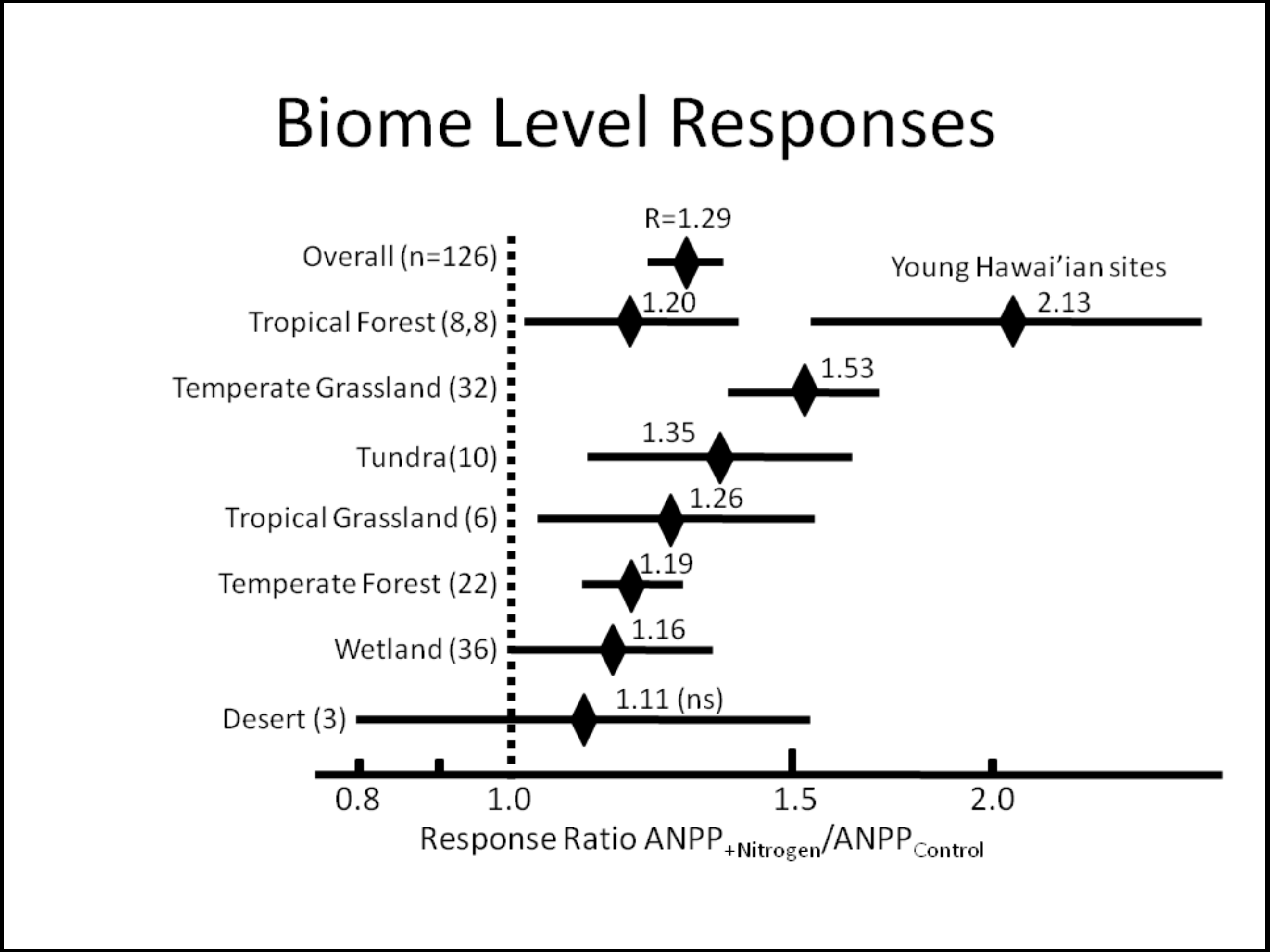
When, where and why does N matter in intact tropical ecosystems?

"The tropics" are not one place!!!



Townsend et al 2008

Fertilization suggests N matters, but there aren't enough data to suggest when, where or why.



LeBauer and Tresider, 2008

Controls of tropical N availability

Inputs: Fixation, Deposition

Outputs: Gas losses, leaching

Internal cycling: mineralization, nitrification, immobilization, DNRA, FEAMMOX…

Controls of tropical N availability

Inputs: Fixation, Deposition

Outputs: Gas losses, leaching

Internal cycling: mineralization, immobilization…

More fixers in the tropics

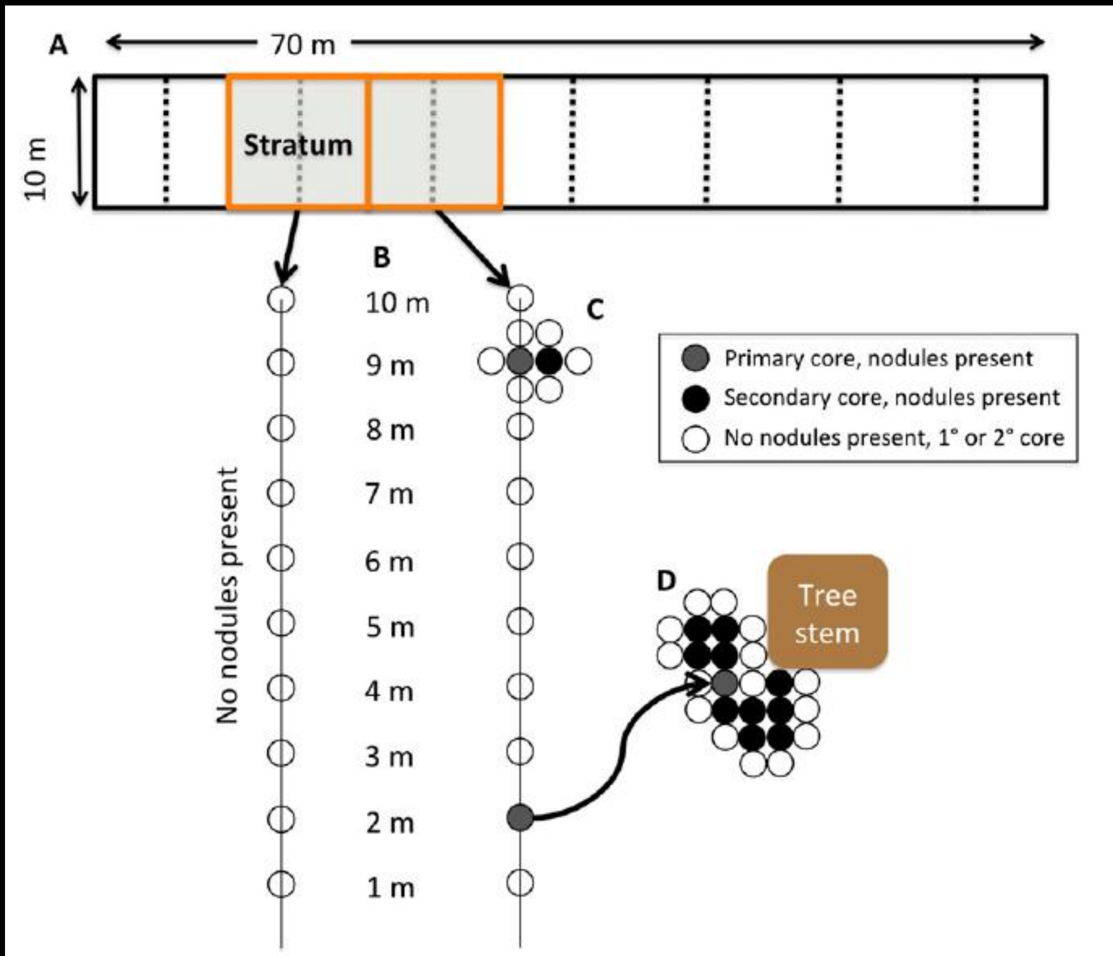
Table 1 Legume abundance in 50-ha plots of various tropical forests worldwide. From Losos & Leigh (2004).

Site	% Basal area	% Trees
Barro Colorado Island, Panama	9.9	7.5
La Planada, Columbia	6.3	5.8
Luquillo, Puerto Rico	6.5	2.7
Yasuni, Ecuador	14.9	13.0
Ituri-Lendo, Democratic Republic of Congo	74.4	11.3
Ituri-Edoro, Democratic Republic of Congo	42.4	15.6
Korup, Cameroon	9.0	5.9
Mudumalai, India	2.4	19.3
Bikut Timah, Singapore	3.5	0.9
Doi Inthanon, Thailand	*	*
Huai Kha Khaeng, Thailand	*	3.1
Palanan, Phillipines	2.3	1.7
Nanjenshan, Taiwan	*	*
Lambir, Malaysia	2.1	2.1
Pasoh, Malaysia	8.5	3.3
Sinharaja, Sri Lanka	*	11.0

*Legumes not present in top 10 families.

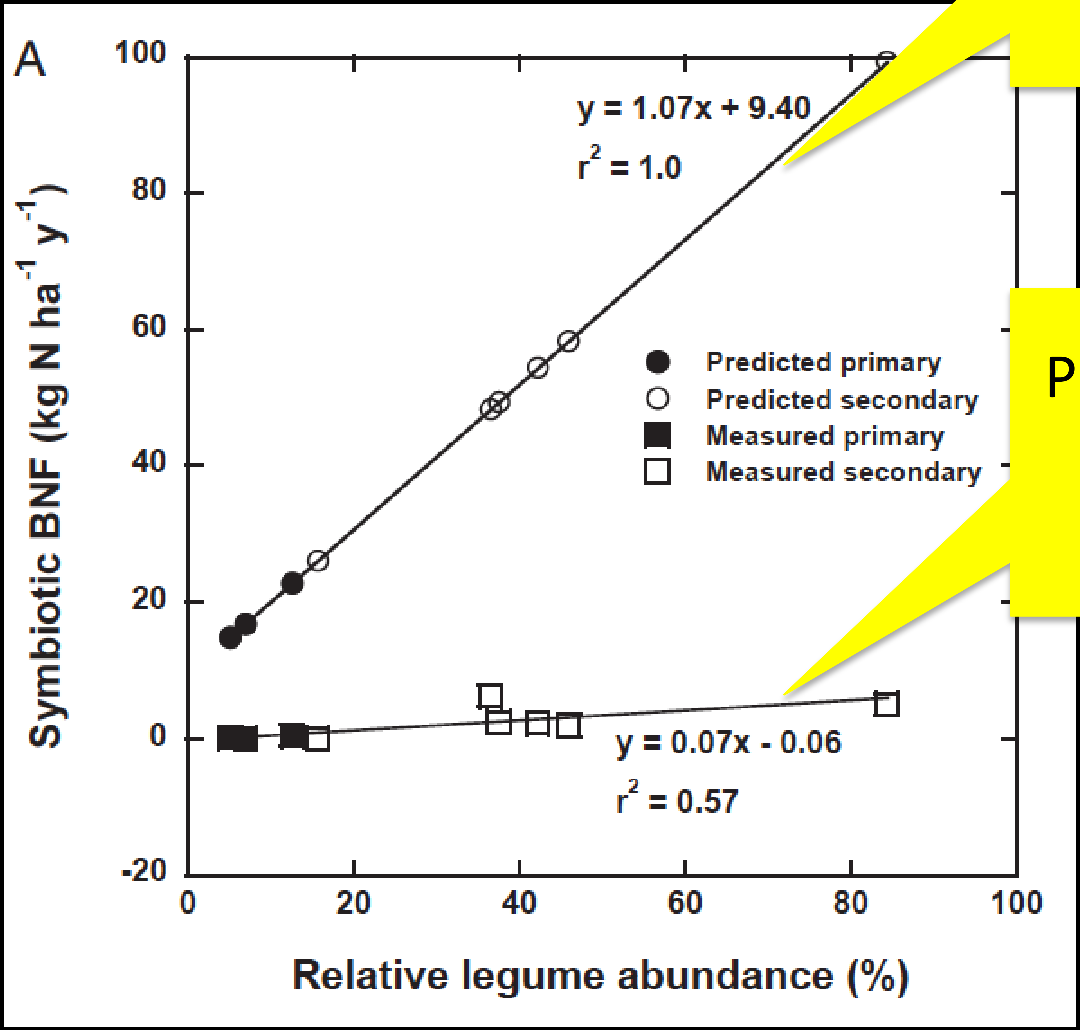
Hedin 2009

But are they fixing?



Sullivan et al, 2014

But are they fixing?

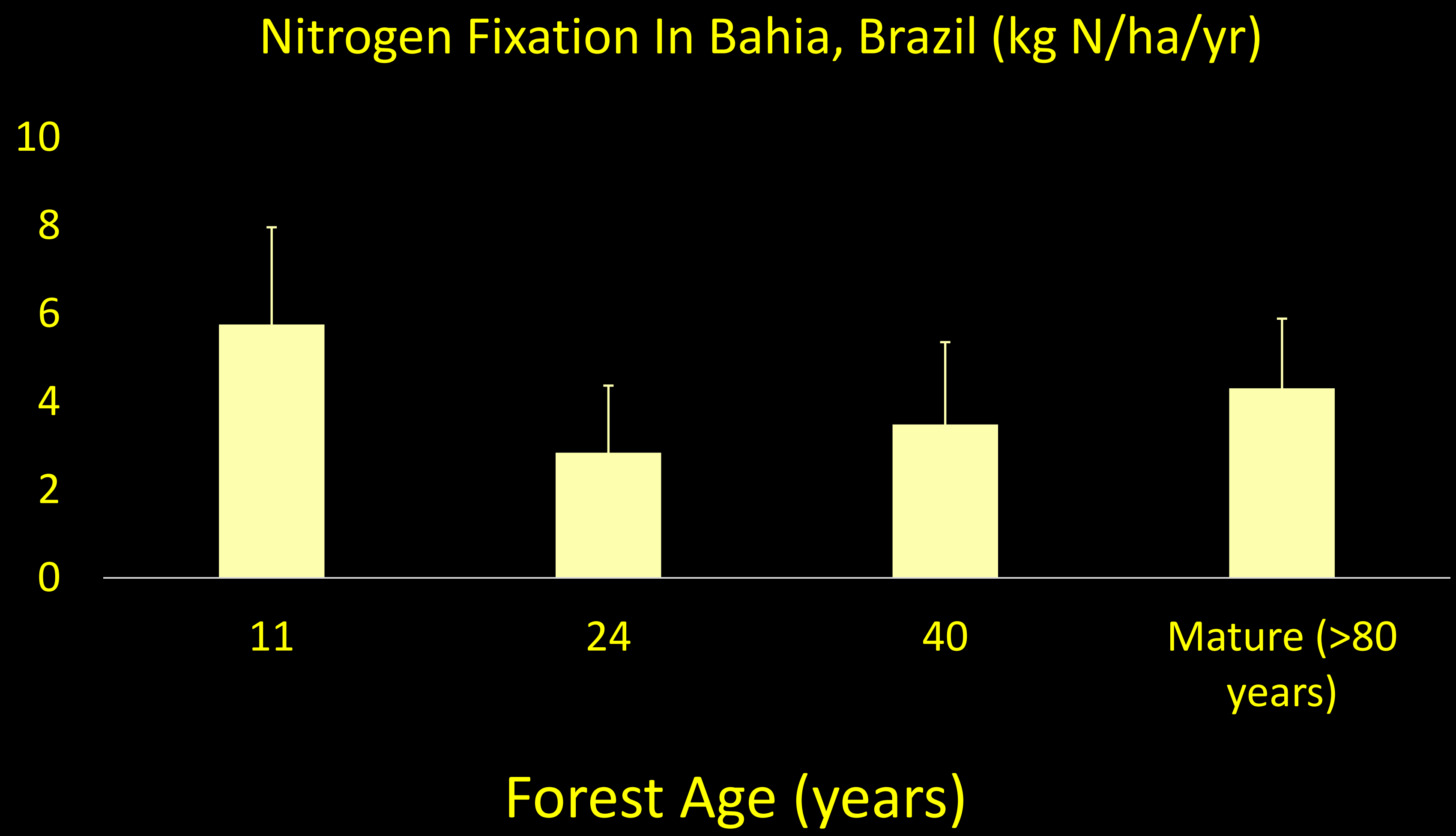


Predicted from legume abundance

Predicted from nodule sampling

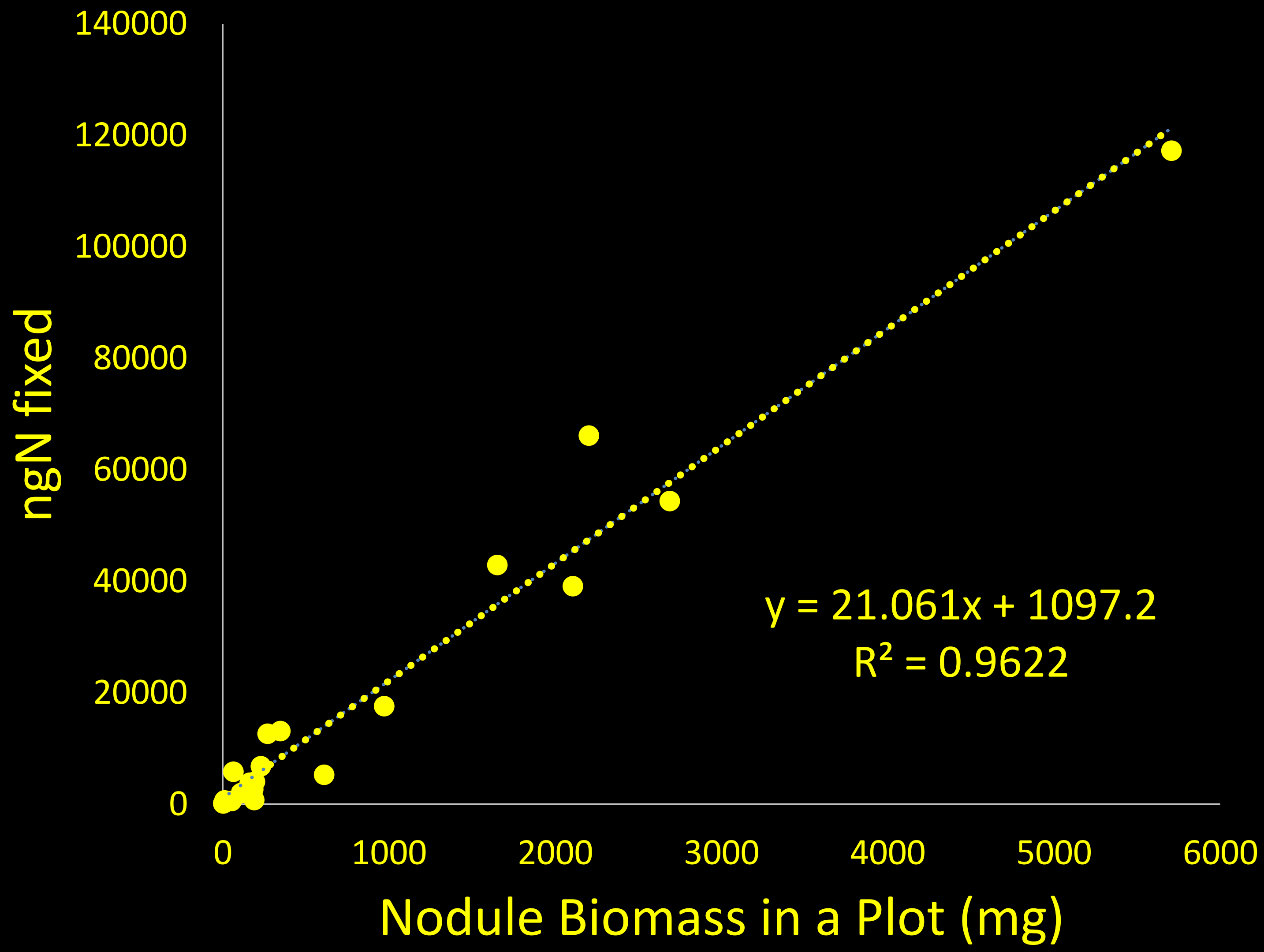
Sullivan et al, 2014

But are they fixing?

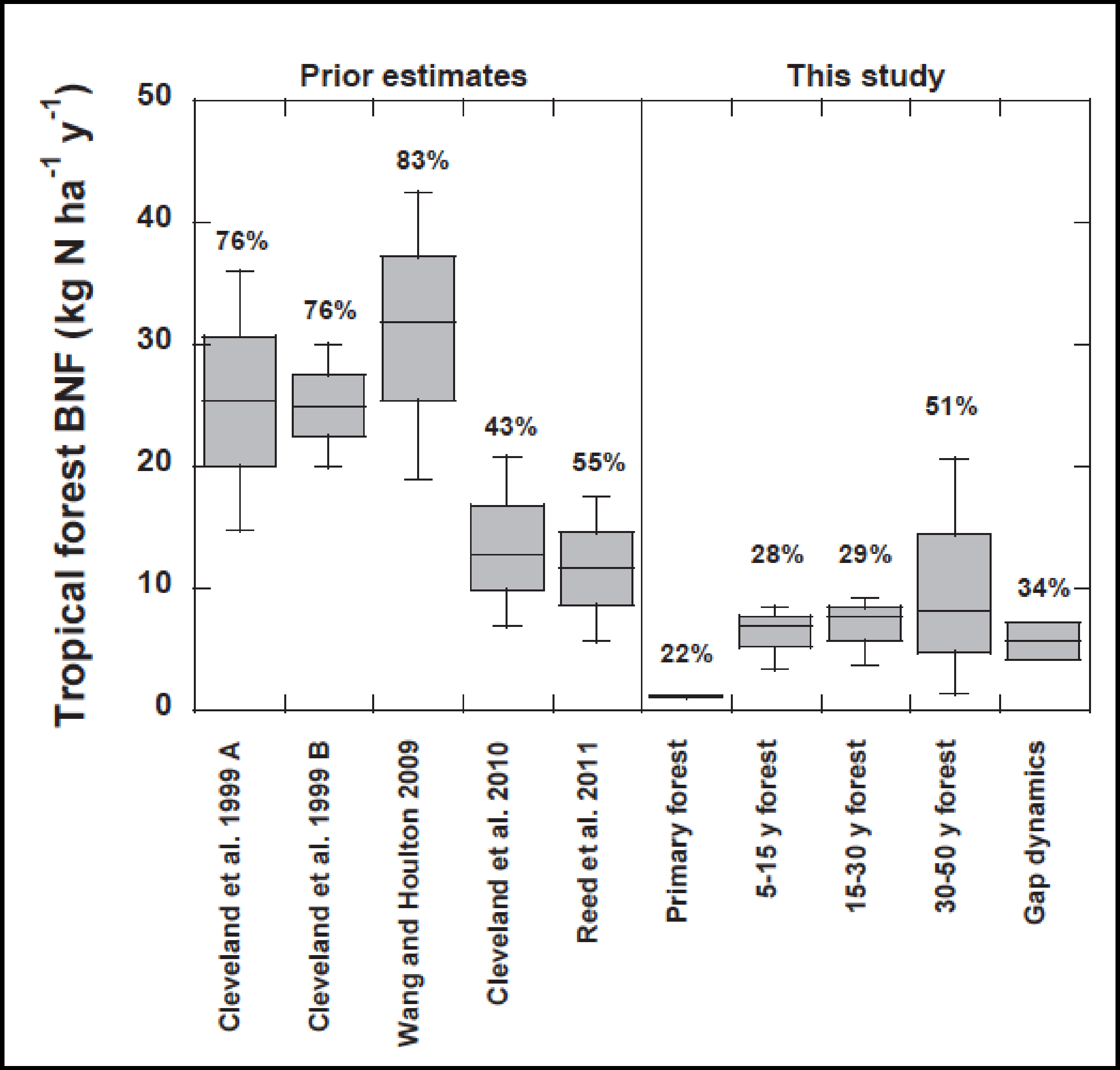


Winbourne unpubl.

Counting legumes doesn't work. Counting nodules does



Our understanding of N inputs is poor



Sullivan et al, 2014

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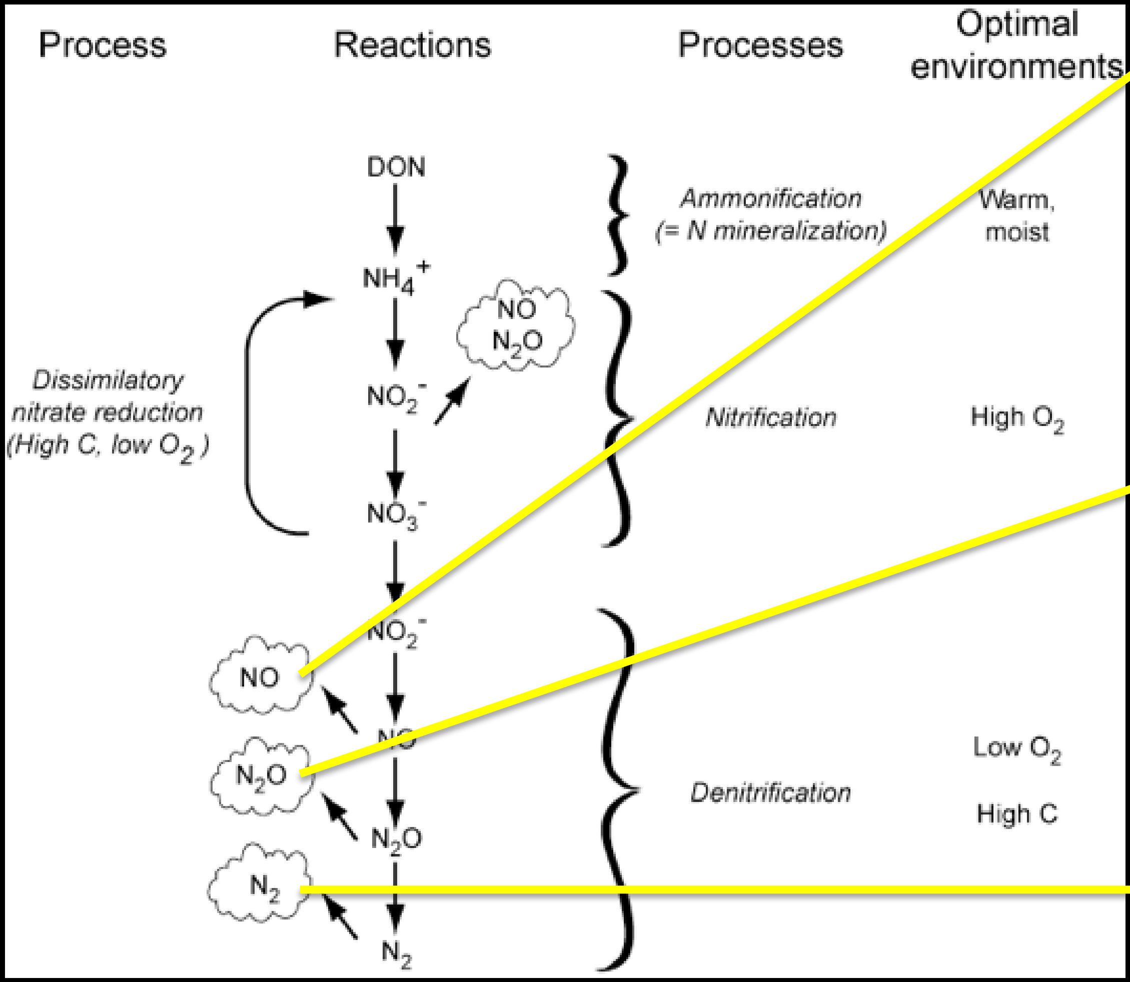
Outputs: Gas losses, leaching

Internal cycling: mineralization, immobilization…

Outputs: Gas losses

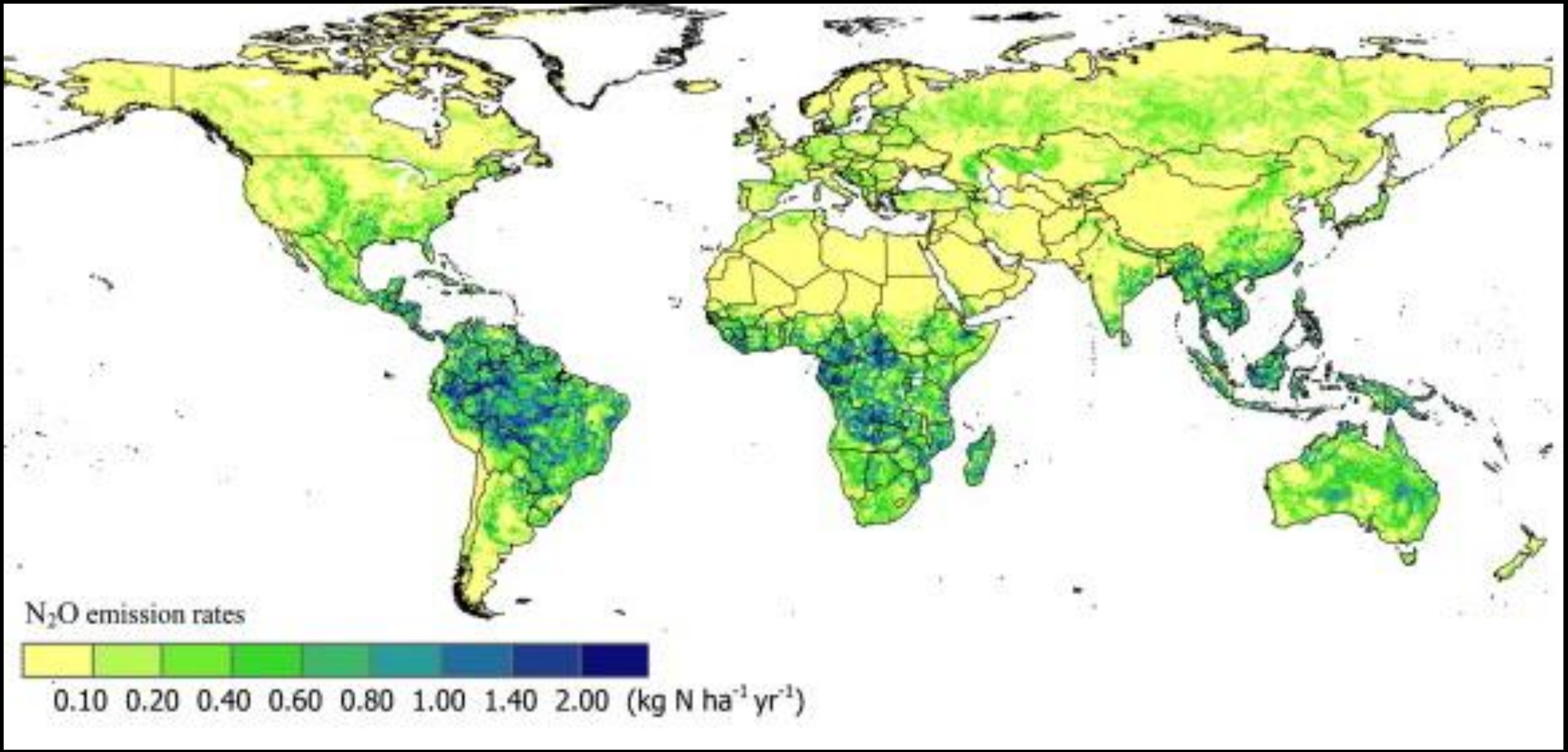


Highly variable in space and time, hard to measure

Highly variable in space and time, “easy”to measure

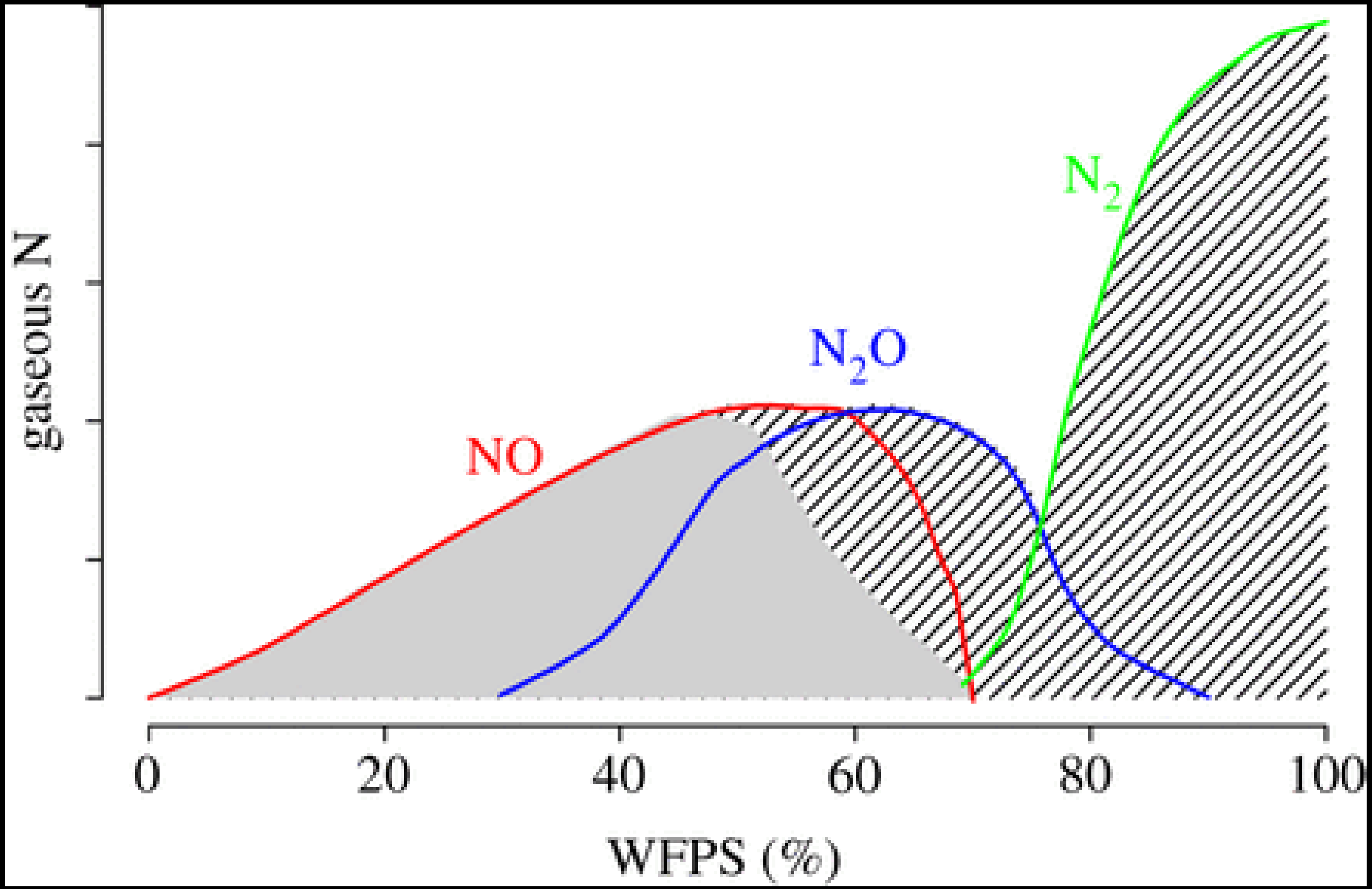
Impossible to measure in the field

Tropical N gas losses: high but poorly constrained, based on N_2O



Zhuang et al. 2012

N_2 losses: Theory

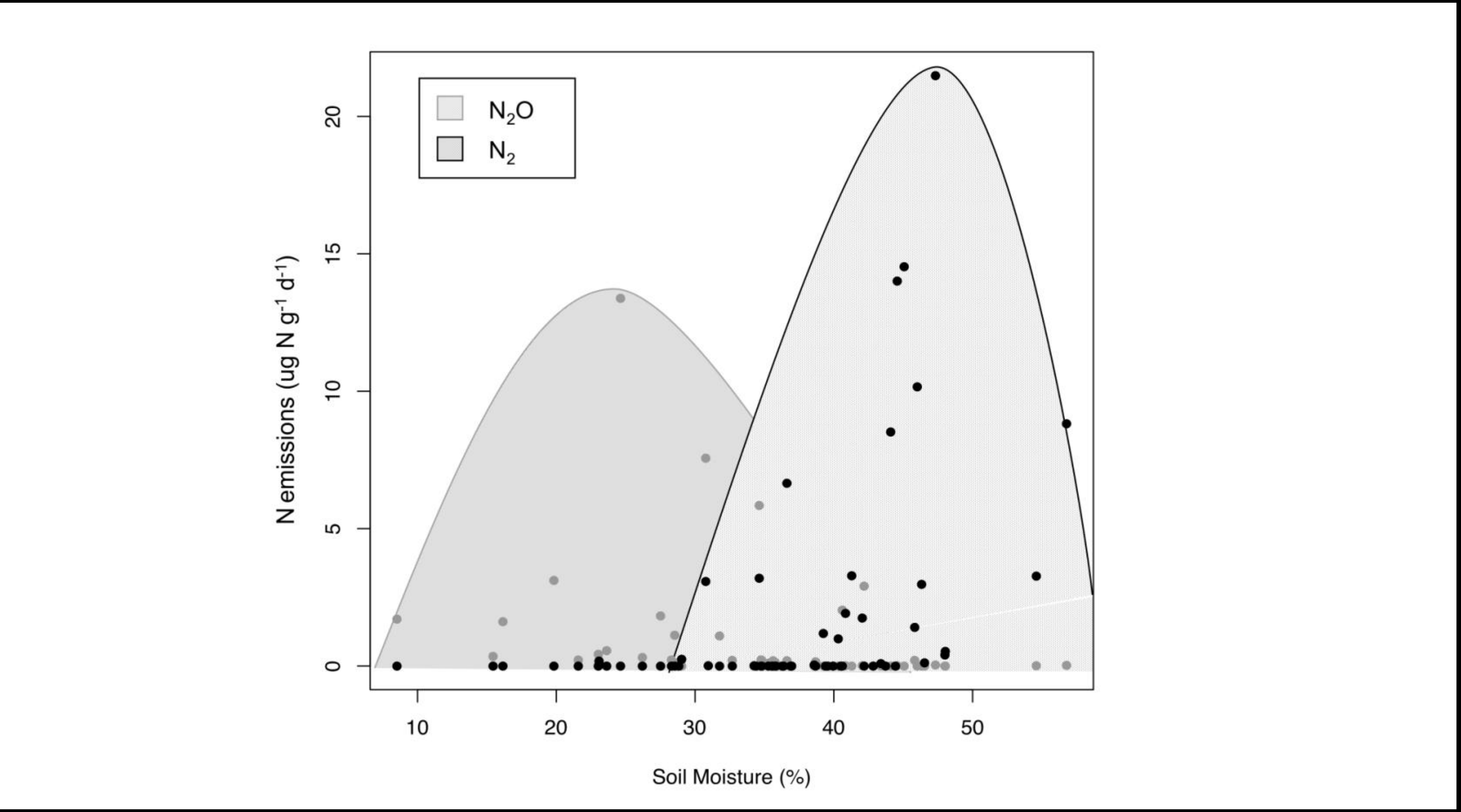


Pilegaard 2013, from Davidson 2000

“Direct” measurement of N_2 emissions

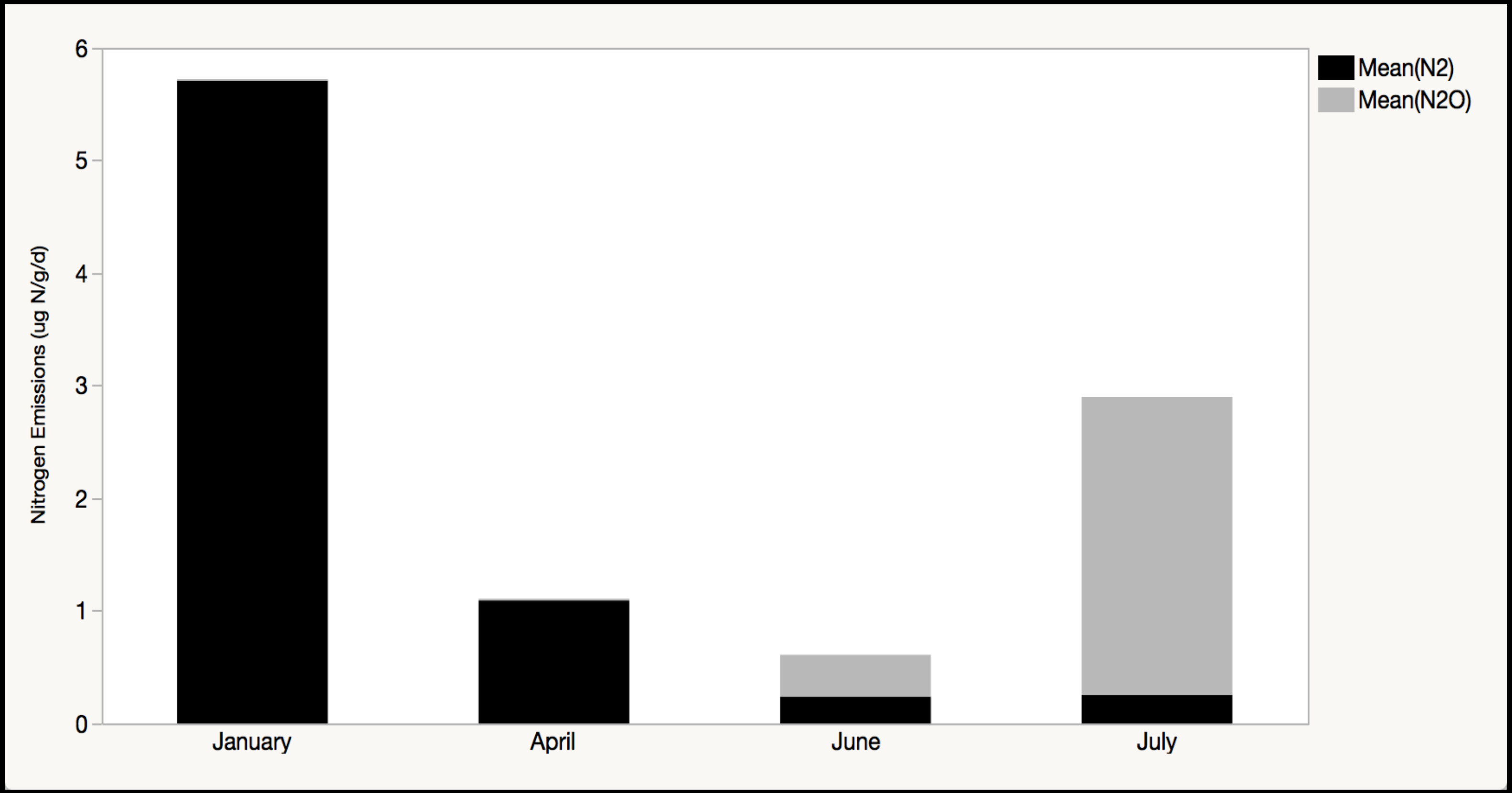
Slide from M. Almaraz

N_2 losses: Data From Puerto Rico



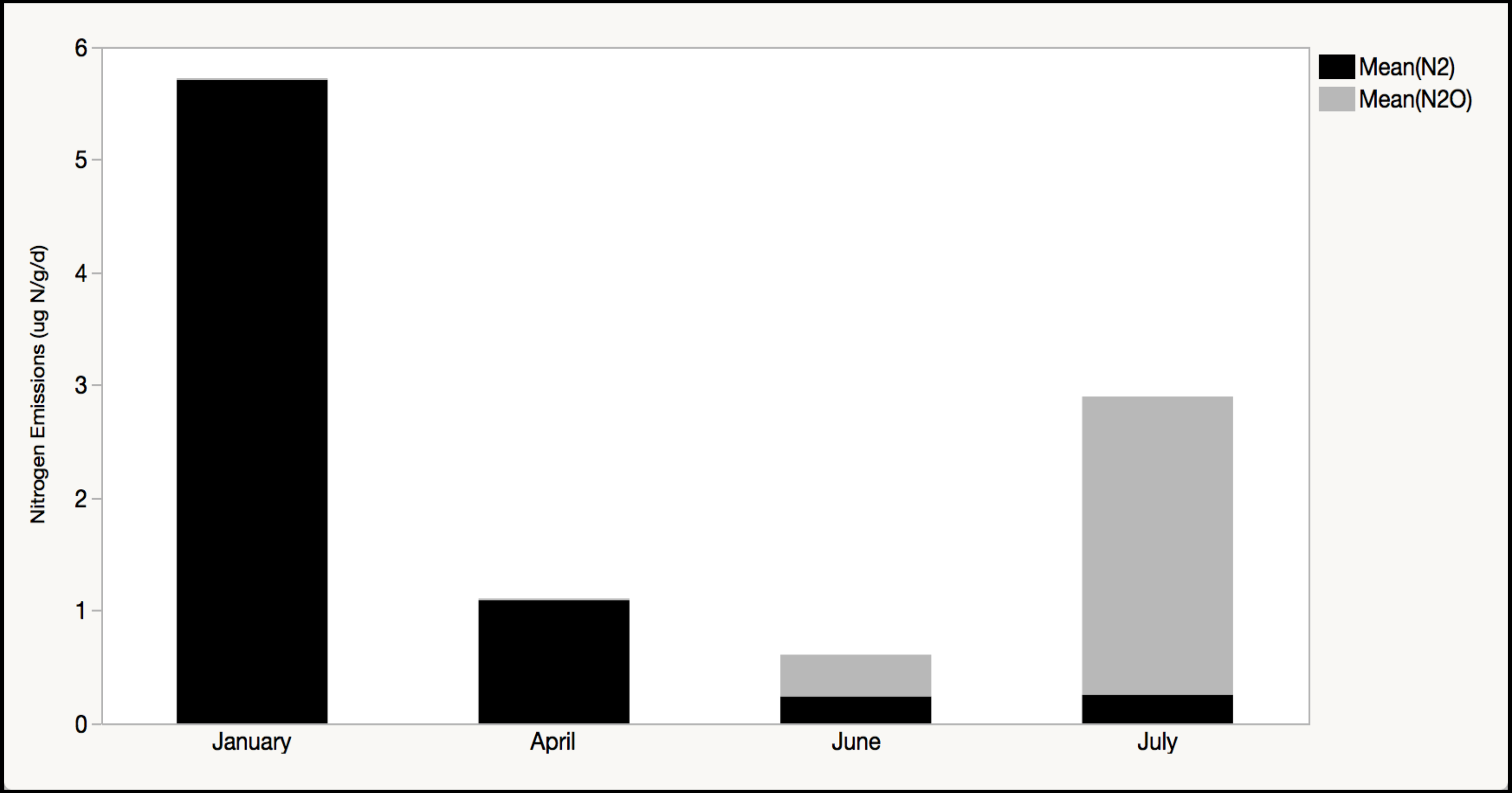
Almaraz unpubl.

N_2 losses ≠ N_2O losses



Almaraz unpubl.

Our understanding of N outputs is poor



Almaraz unpubl.

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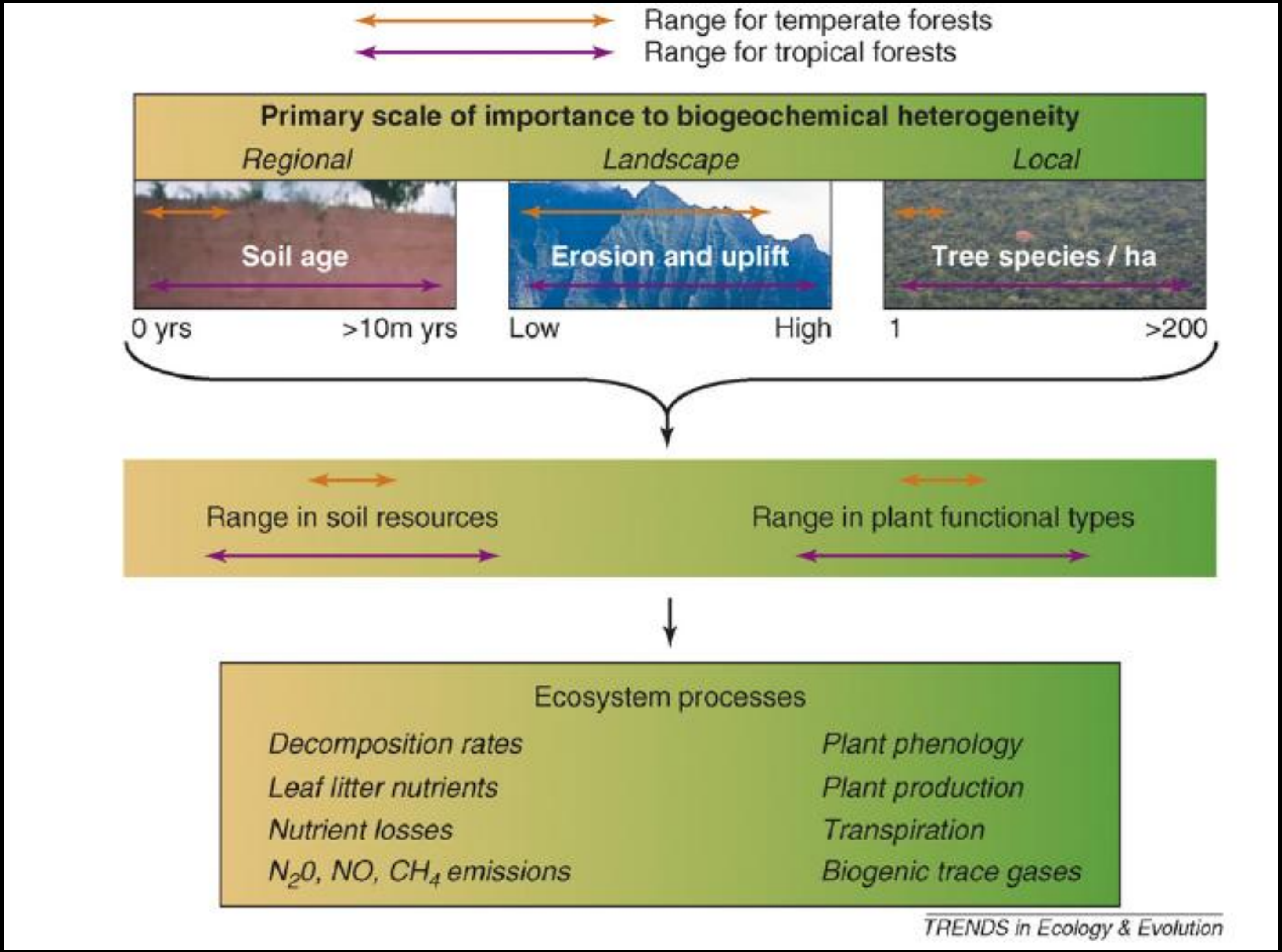


Townsend et al 2008

Heterogeneity is challenging

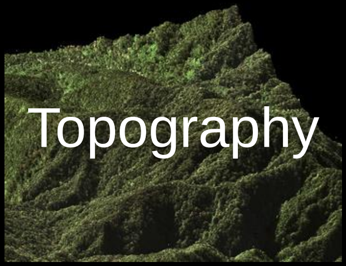
Time	Climate	Parent material	Topograph y	Organisms

N availability

Heterogeneity is challenging

Time

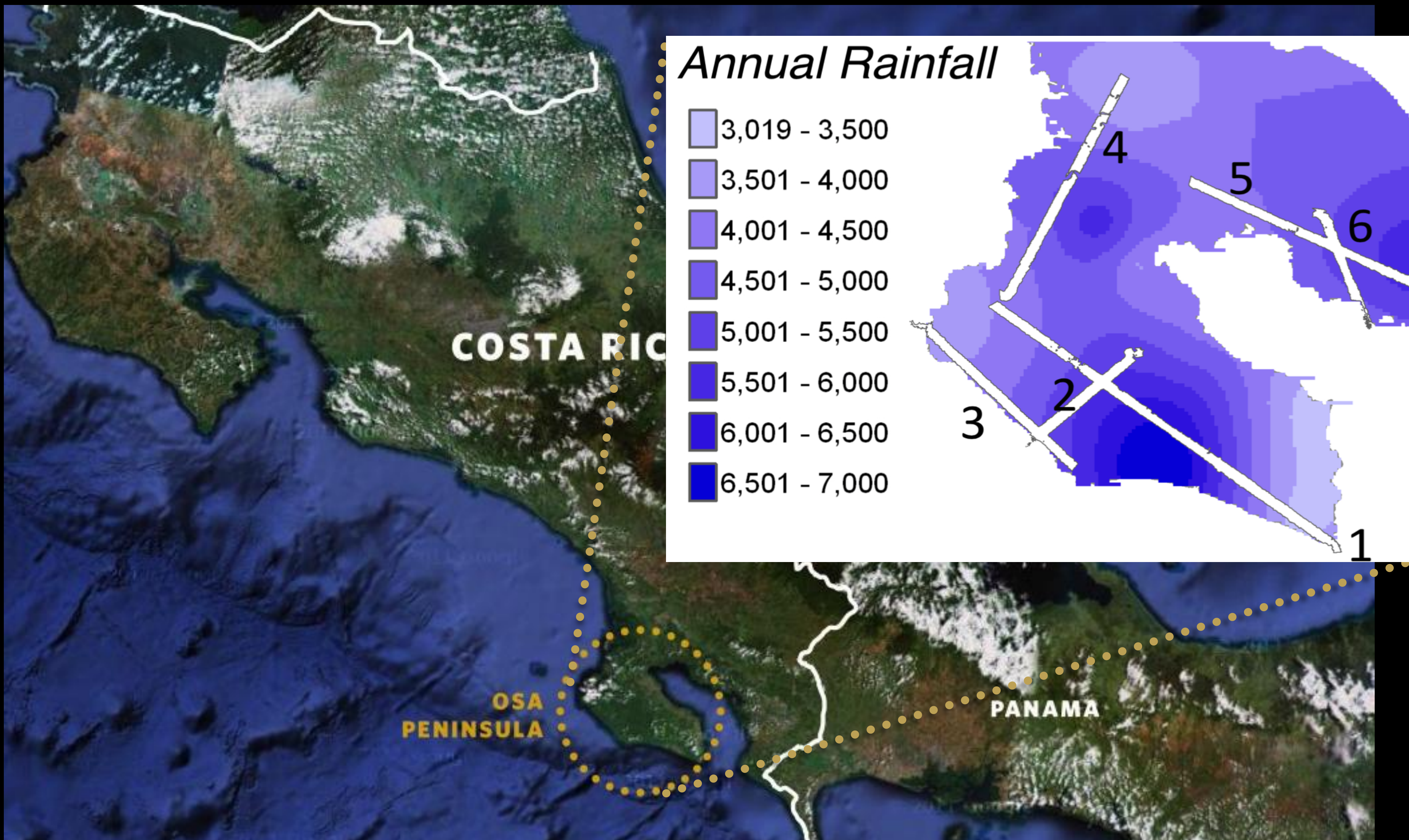
Parent material



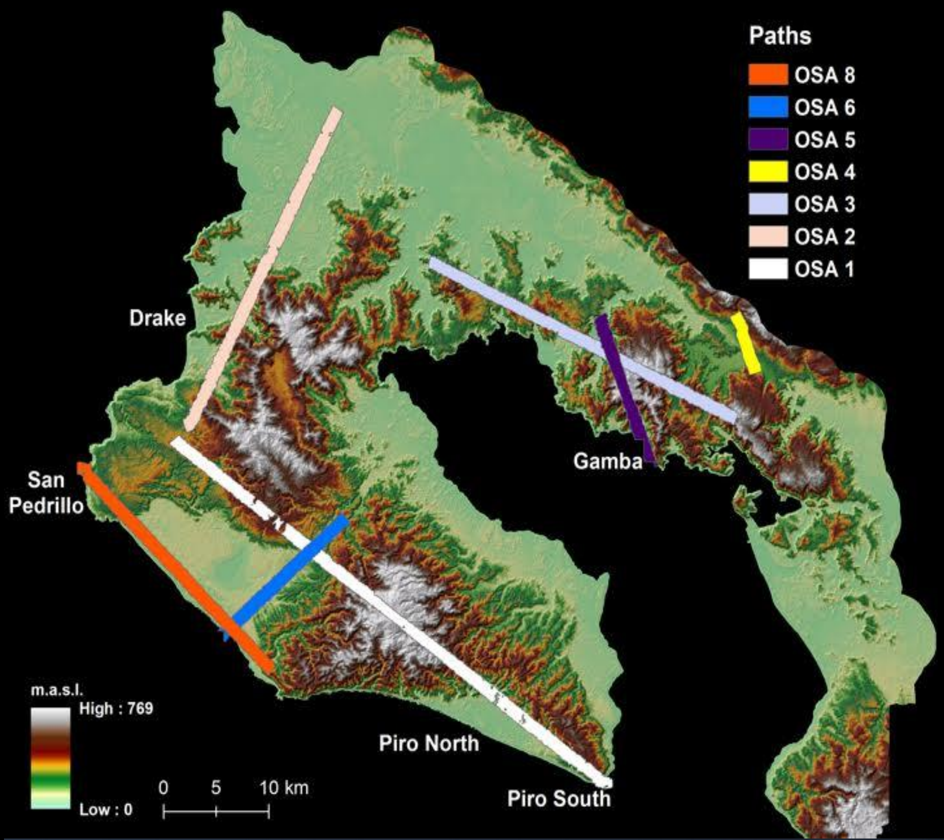
N availability

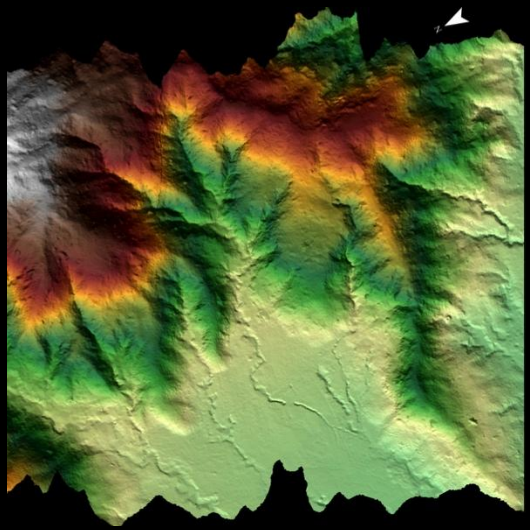
How do topography, rainfall, and foliar N influence N availability?

The Osa Peninsula, Costa Rica

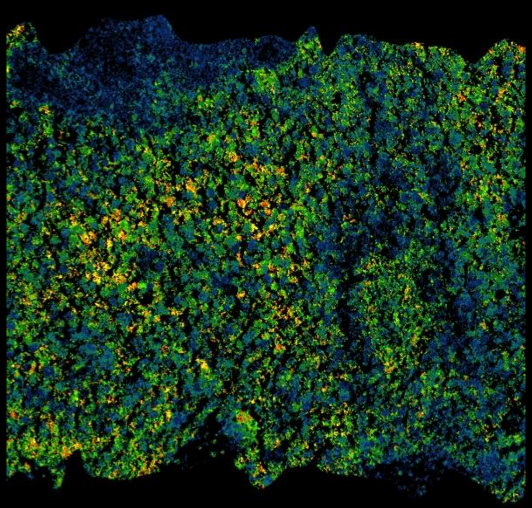


Hyperspectral-derived canopy N
Lidar derived topography



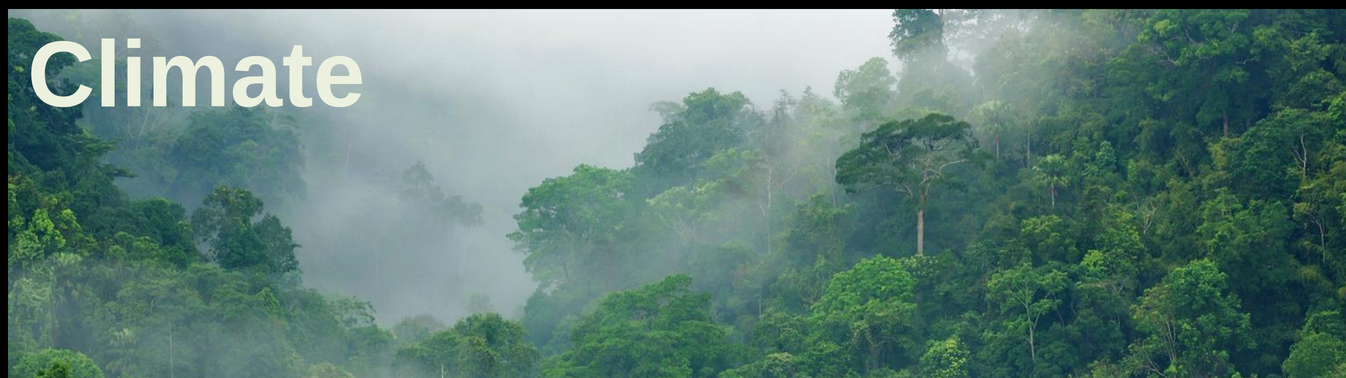


Digital Elevation Models

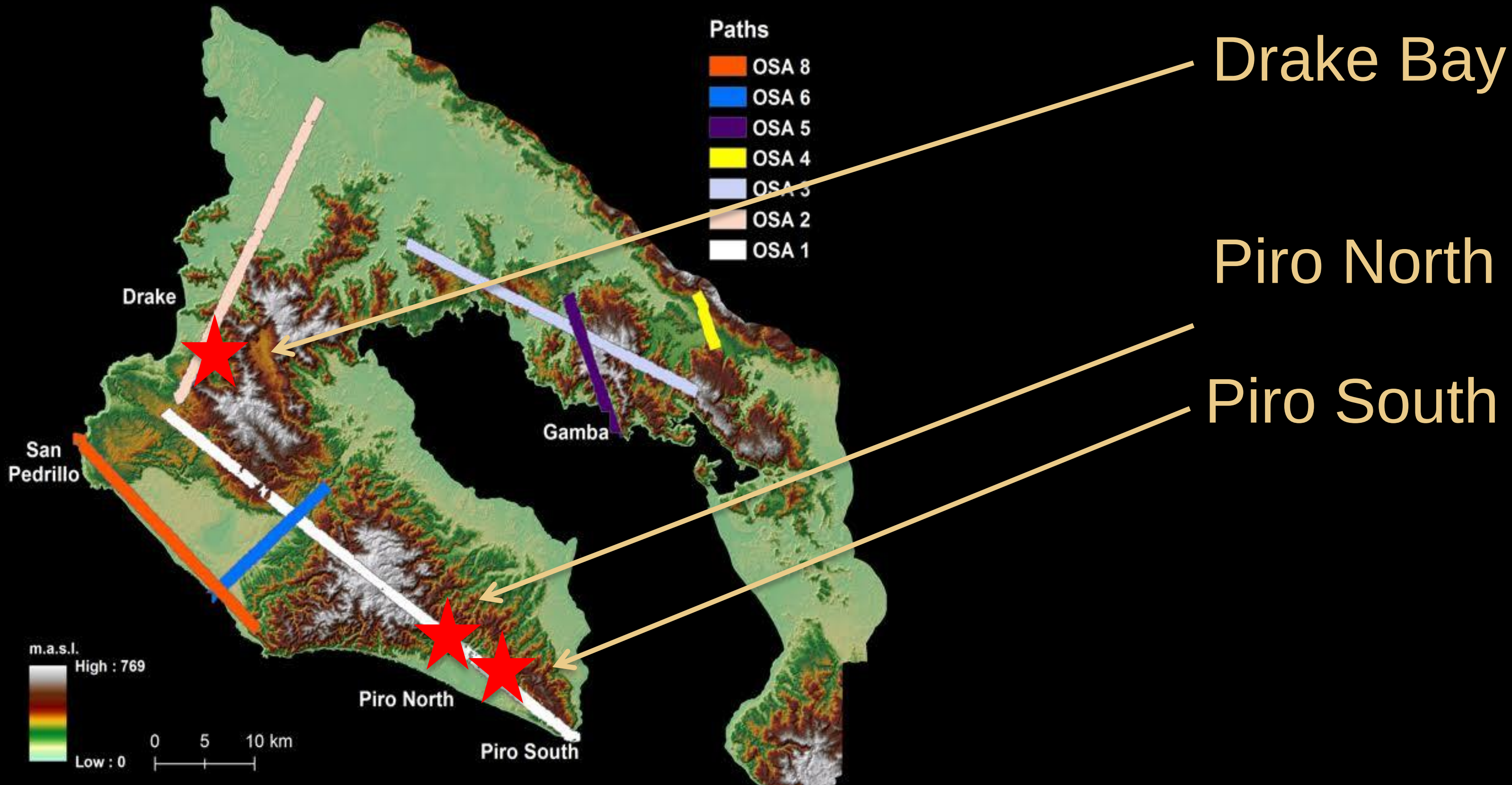


Foliar Nitrogen Maps


Topography


Climate

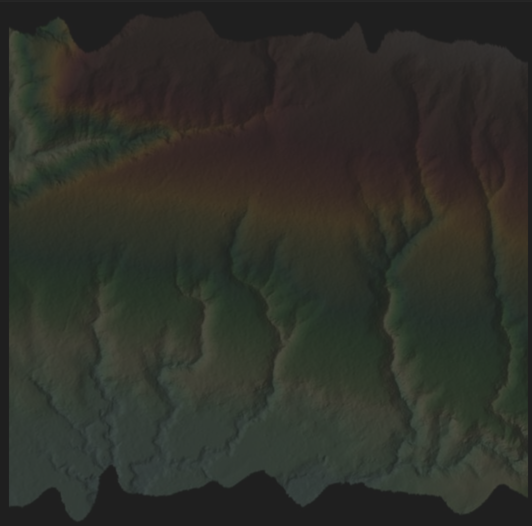
Variation in topography, climate.



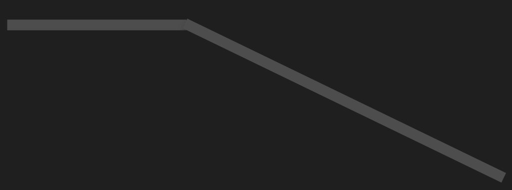
CARNEGIE AIRBORNE OBSERVATORY

Topography

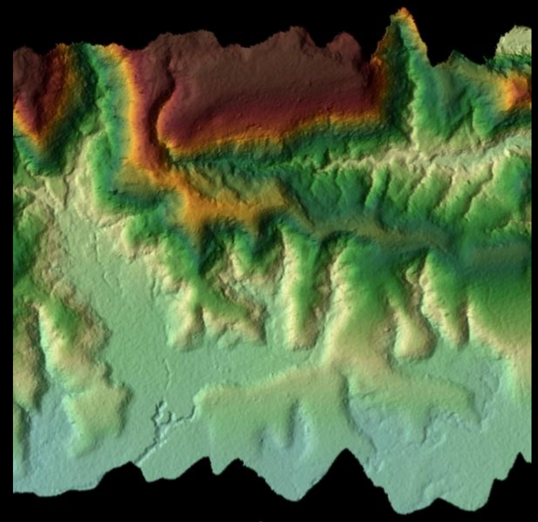
Piro South



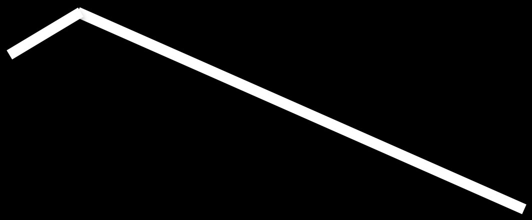
Broad, flat ridge



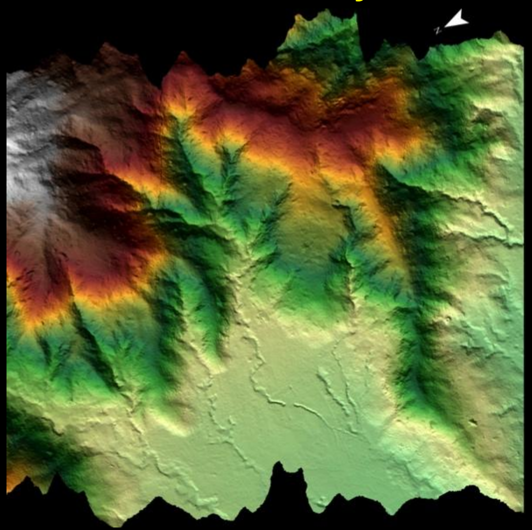
Piro North



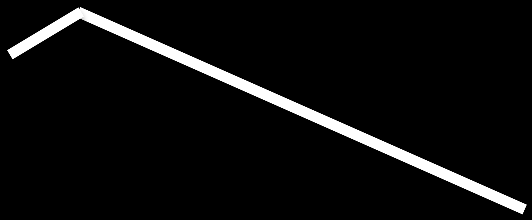
Narrow ridge



Drake Bay

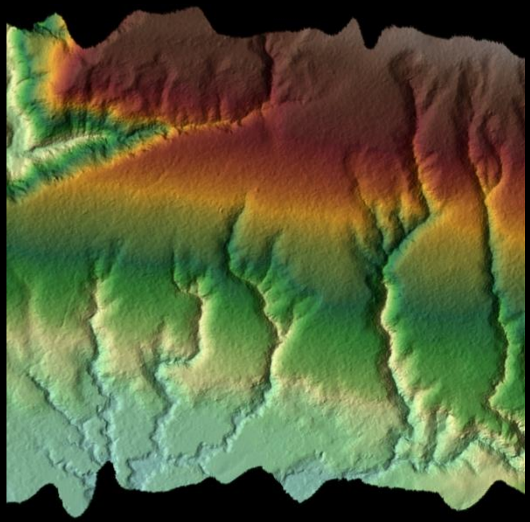


Narrow ridge

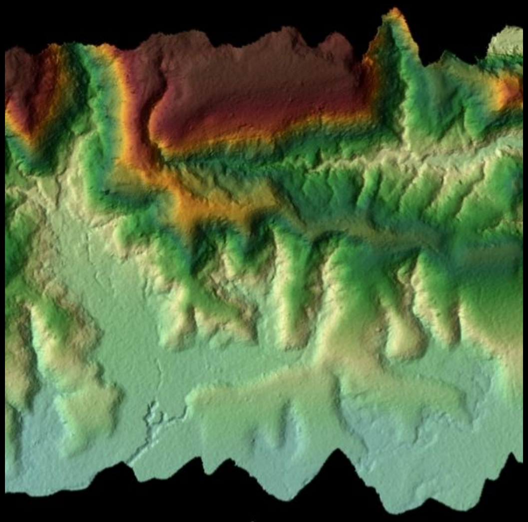


Topography

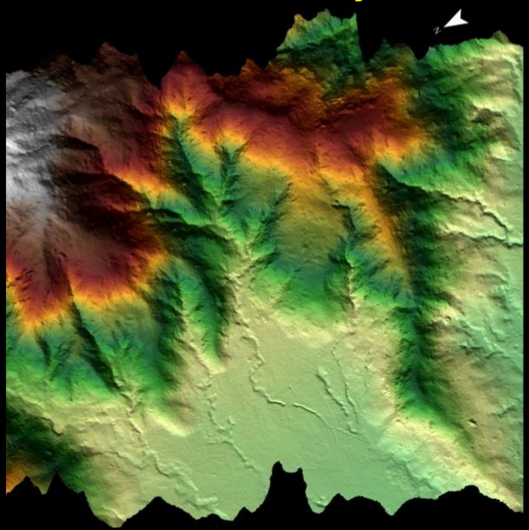
Piro South



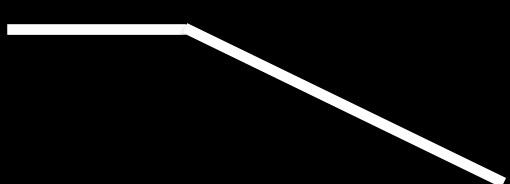
Piro North



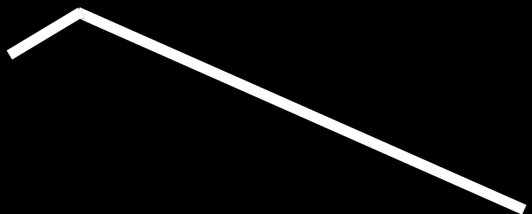
Drake Bay



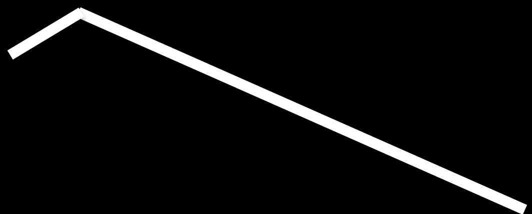
Broad, flat ridge



Narrow ridge

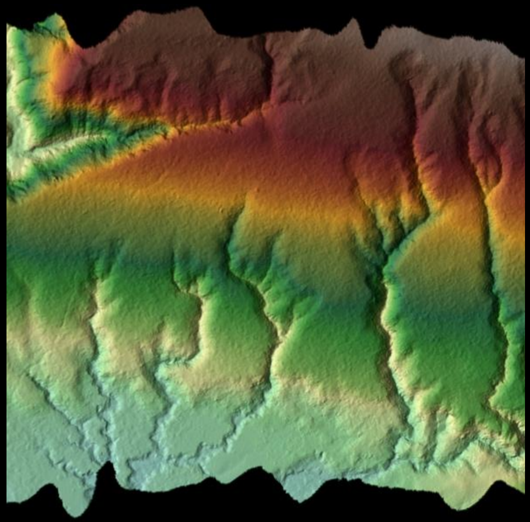


Narrow ridge

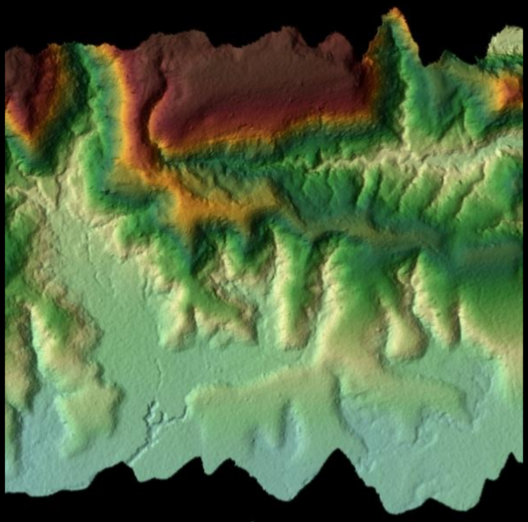


Climate

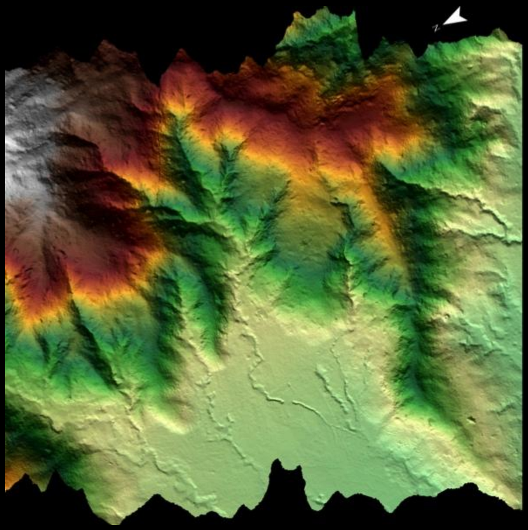
Piro South



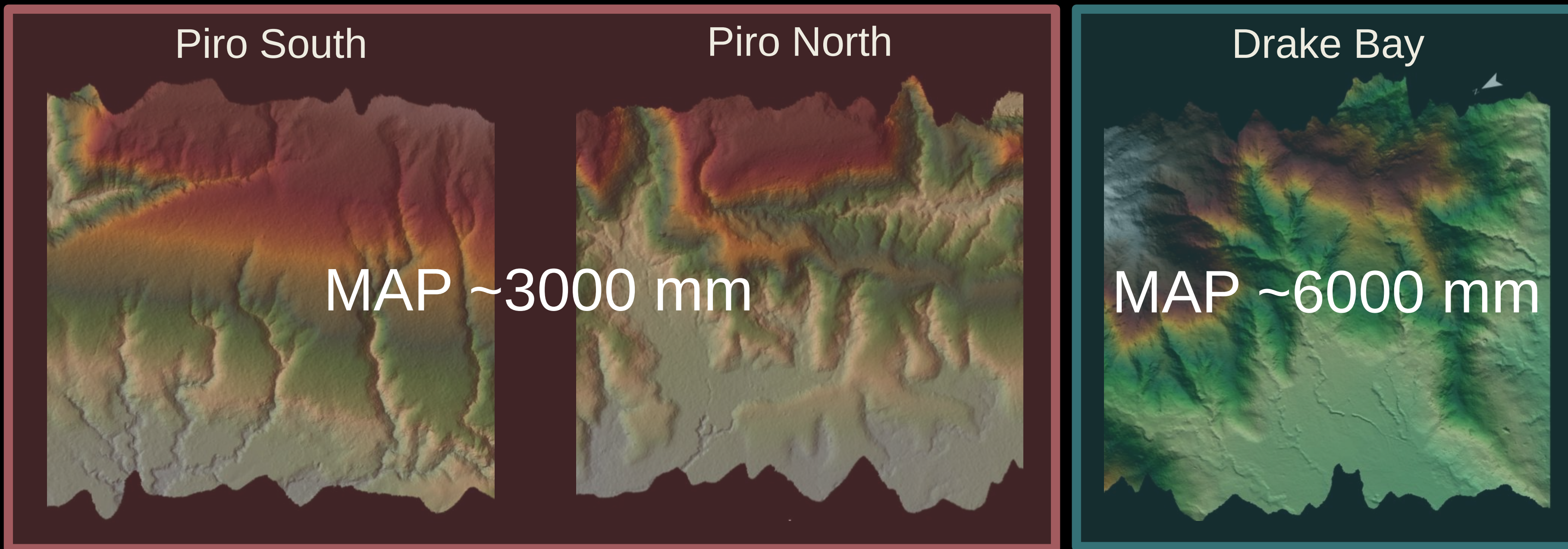
Piro North



Drake Bay

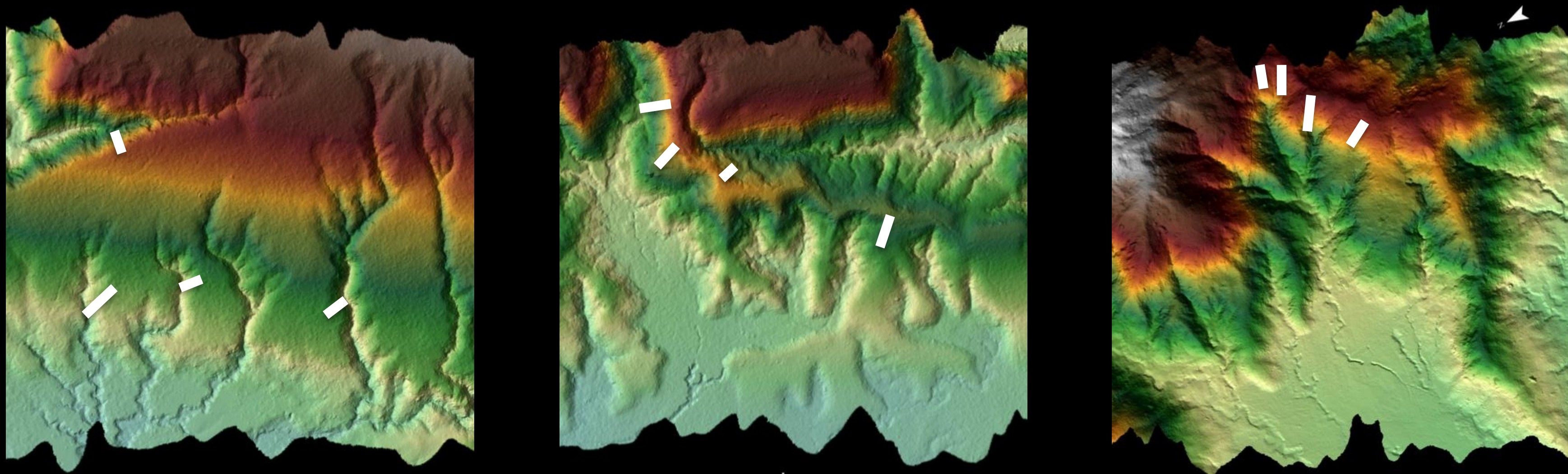


Climate

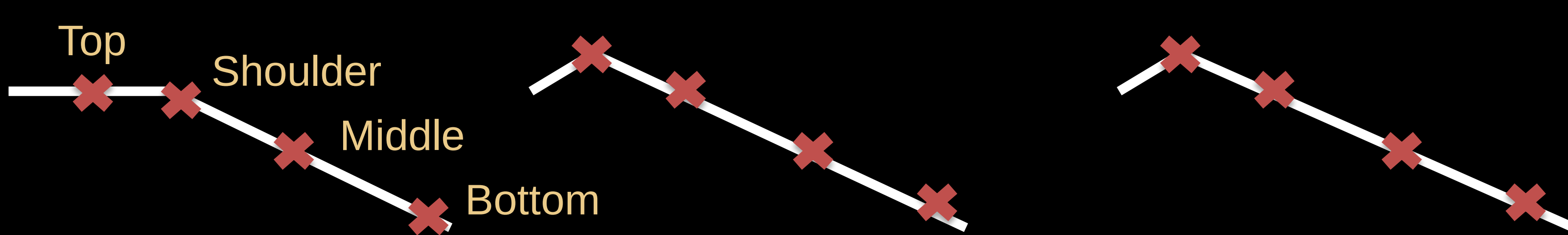


Sample collection & analyses

Piro South | Piro North | Drake Bay

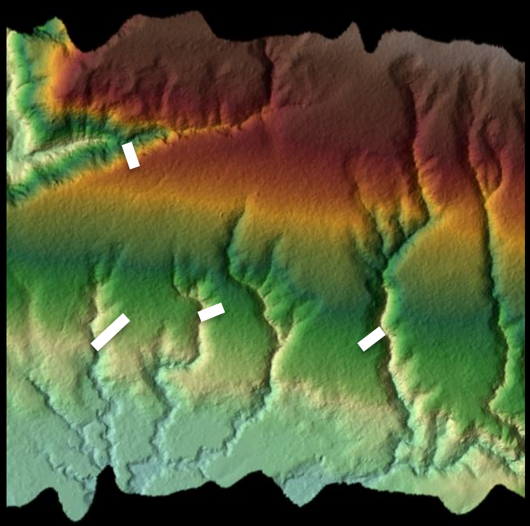


- 3 regions x 4 catenas x 4 transects x 2 seasons

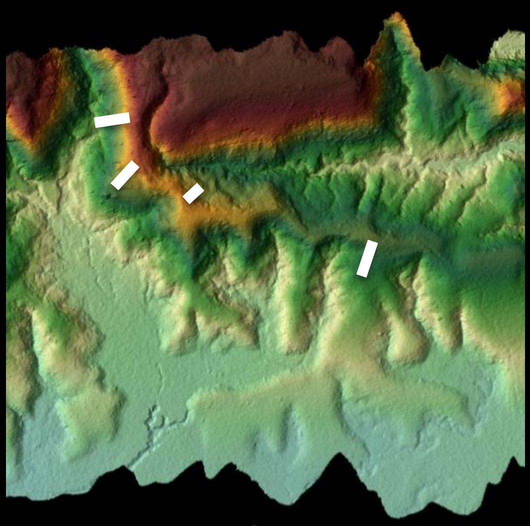


N metrics measured

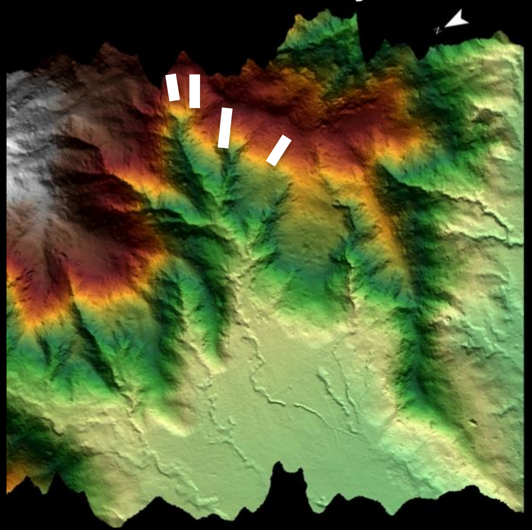
Piro South



Piro North



Drake Bay

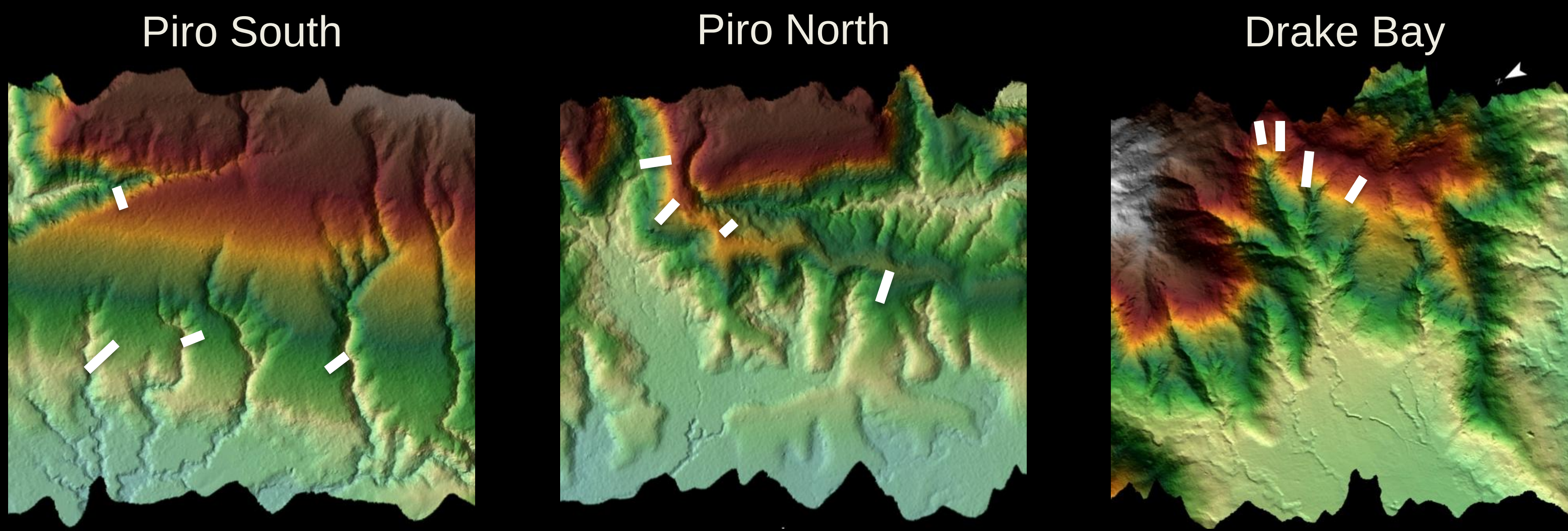


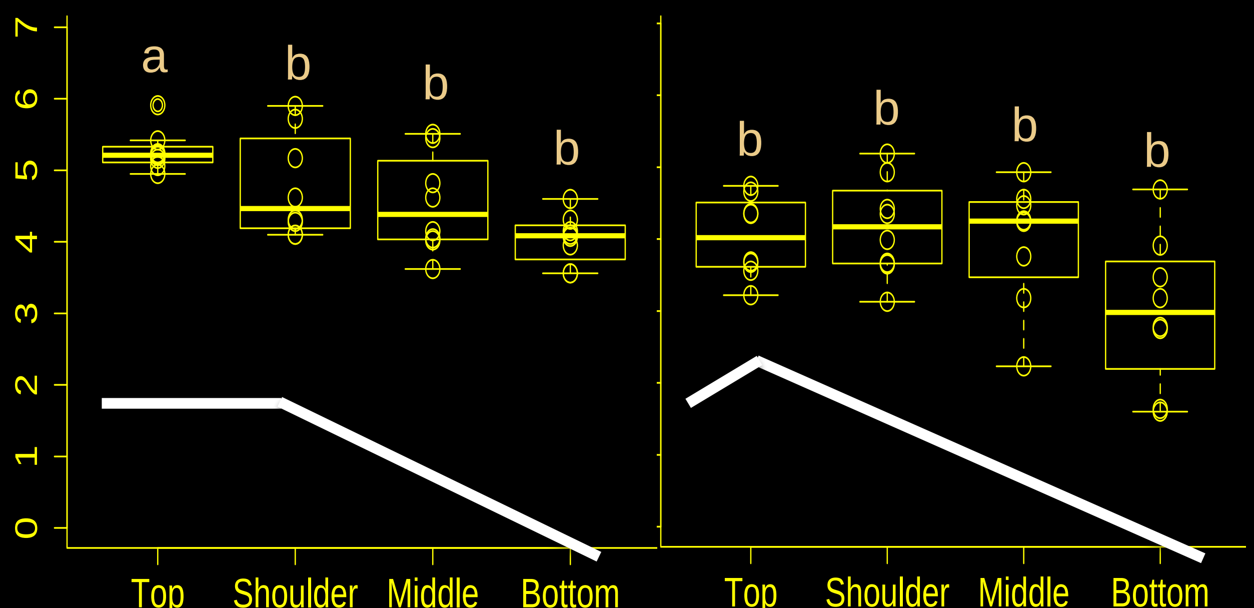
NO_3^--N and NH_4^+-N → Instantaneous

Net nitrification
Net N mineralization → 5 days

$\delta^{15}N$ → 100s – 1000s of years

Topography ($\delta^{15}N$ o/oo)

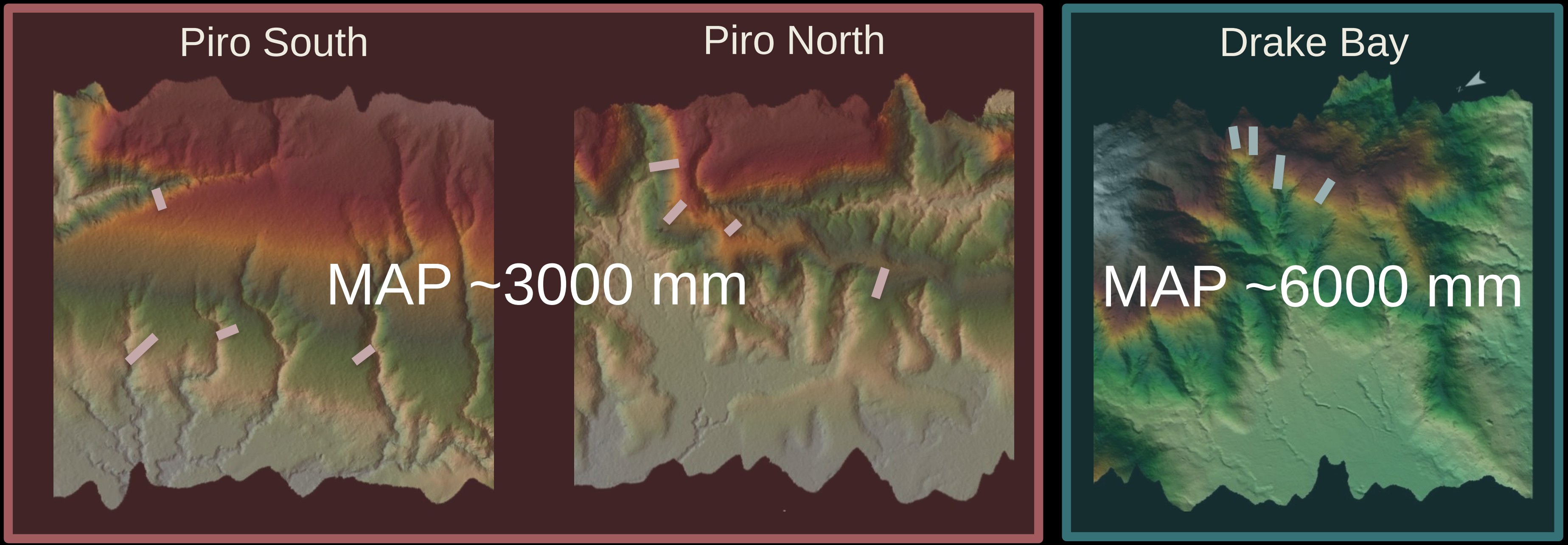




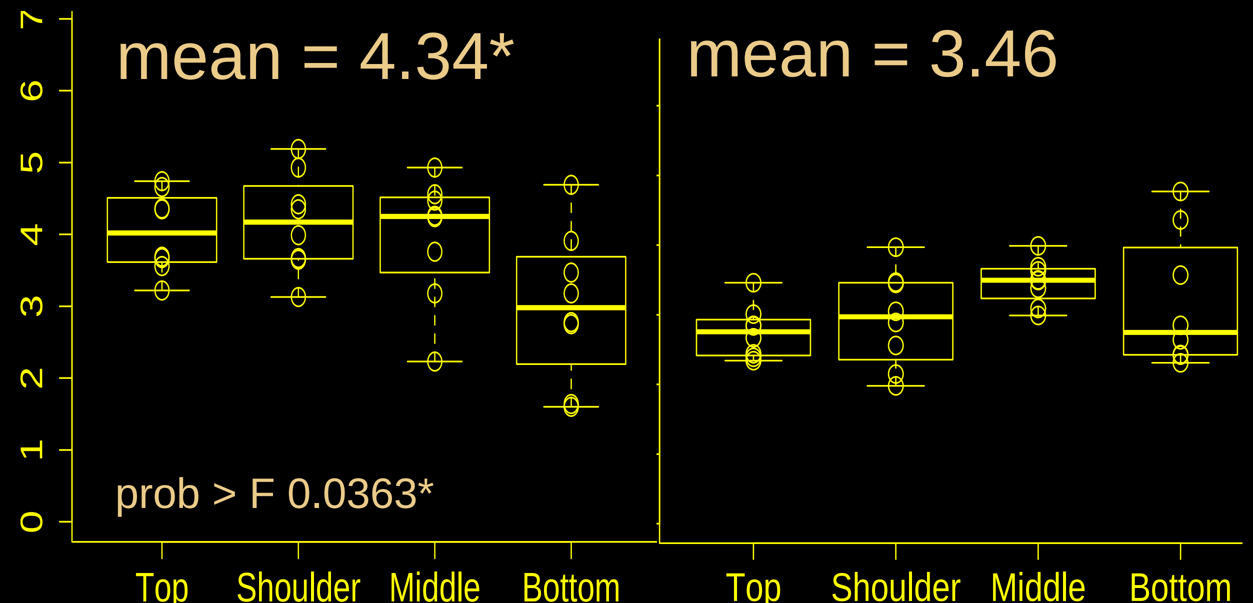
δ15N was elevated on broad, flat ridges.

Osborne et al, in revision

Climate ($\delta^{15}N$ o/oo)



δ15N was elevated under drier conditions.



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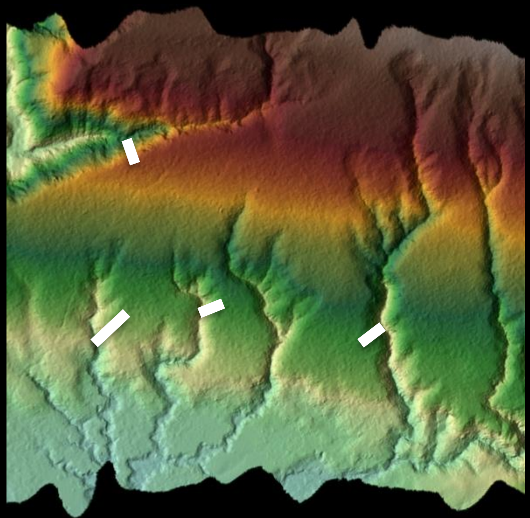
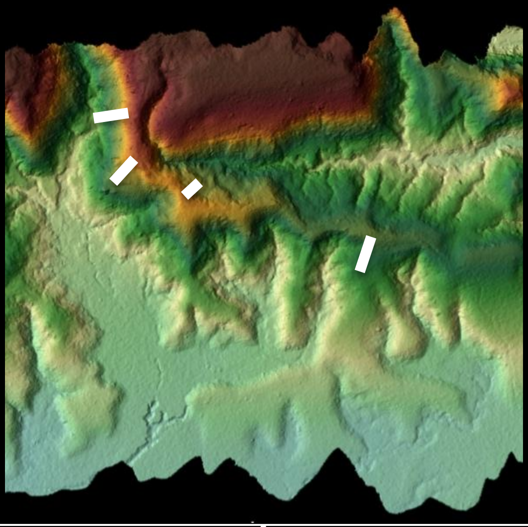
Topography and climate summary

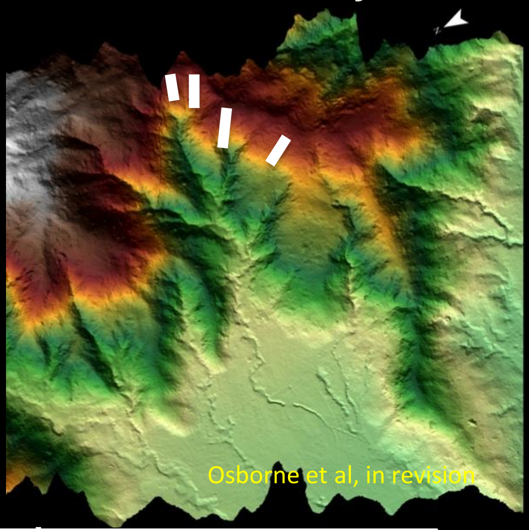
Piro South



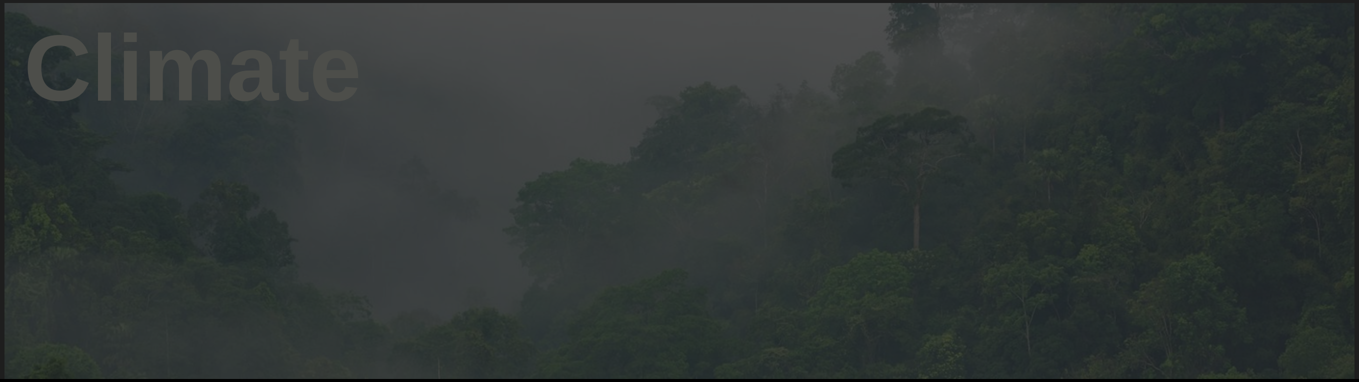
Piro North



Drake Bay

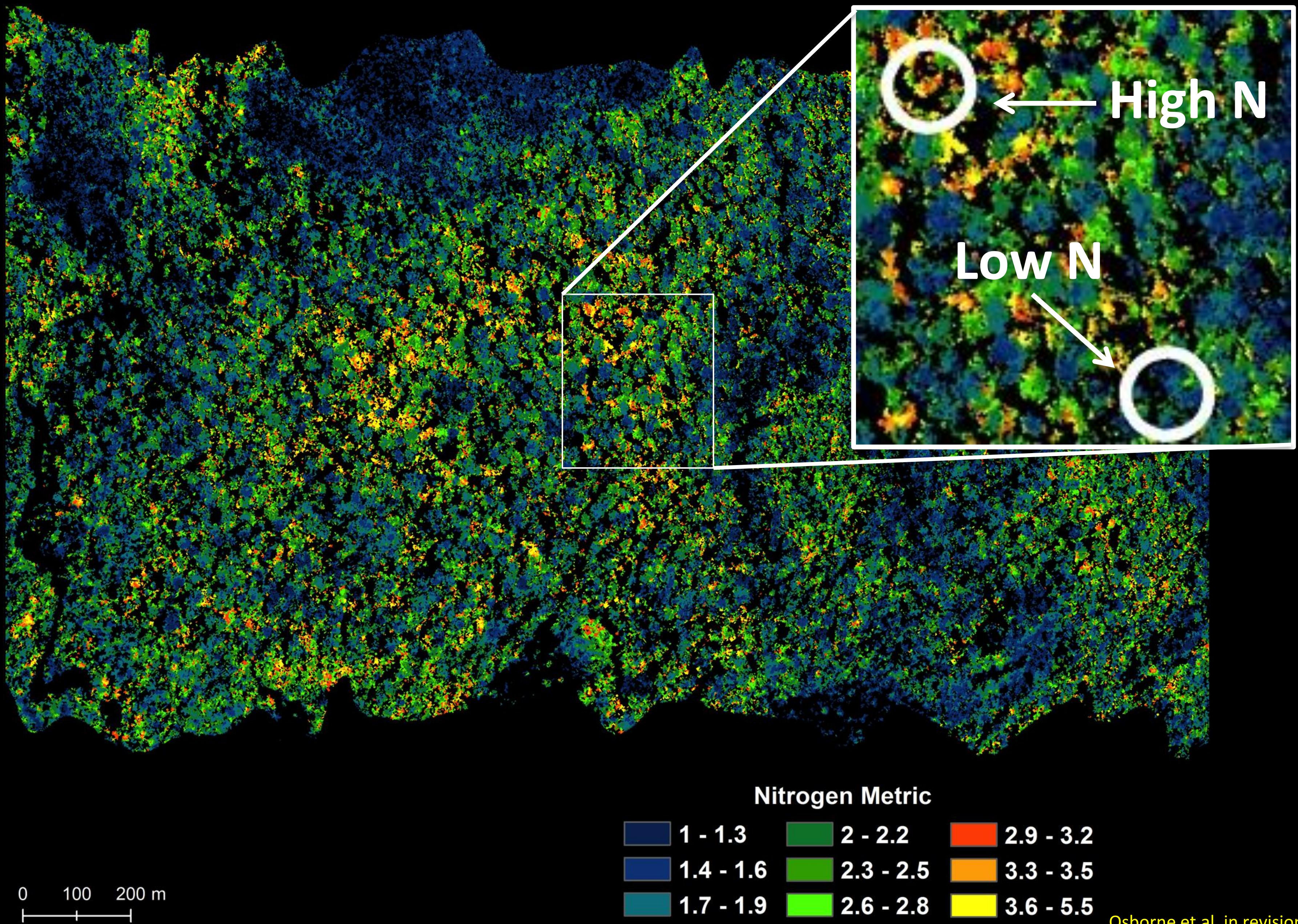


	Climate effect	Topography effect
NO_3^--N and NH_4^+-N	✗	✗
NO_3^--N and NH_4^+-N	✗	✗
$\delta^{15}N$	✔	✔


Topography

Climate

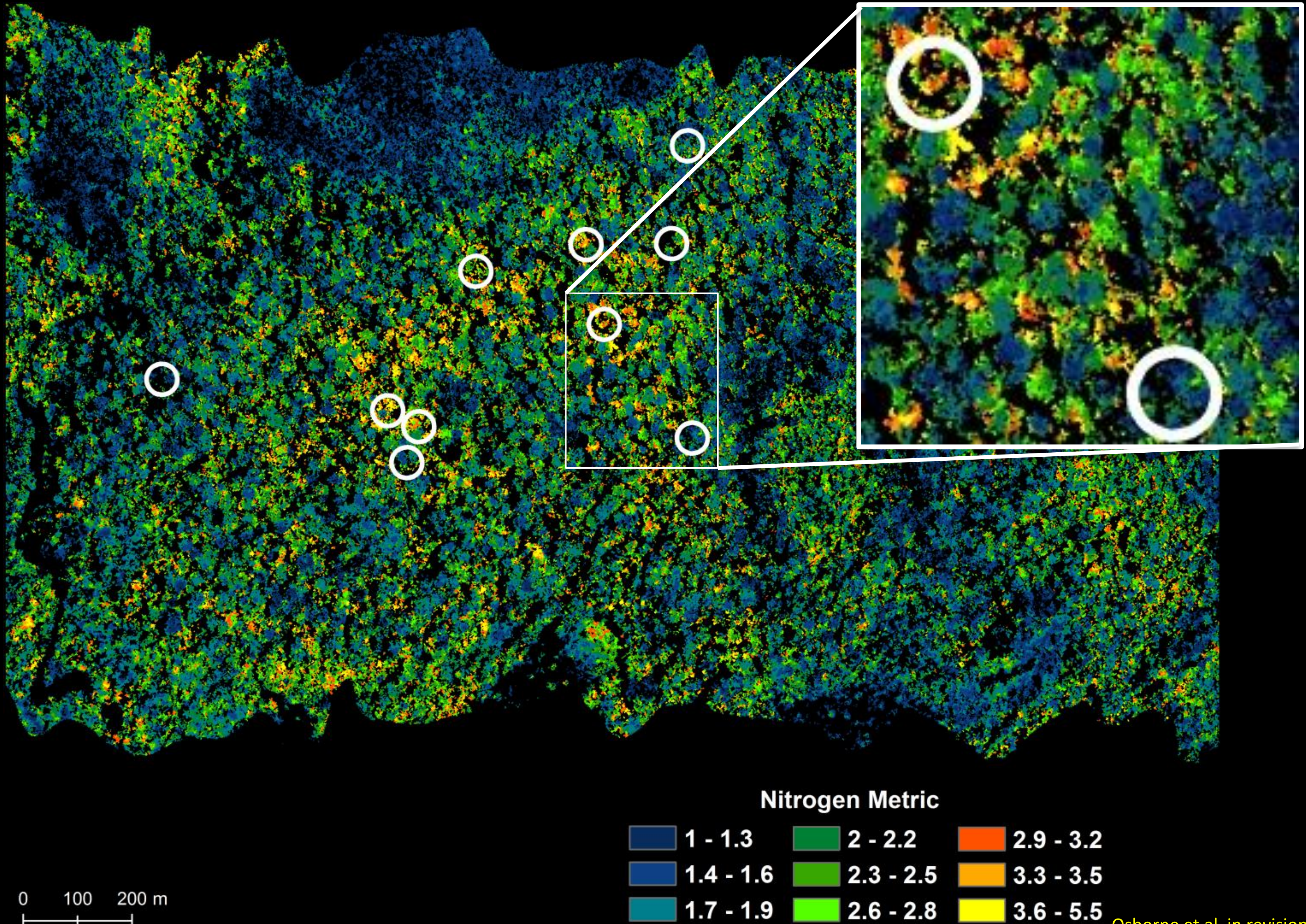
Organisms

Organisms



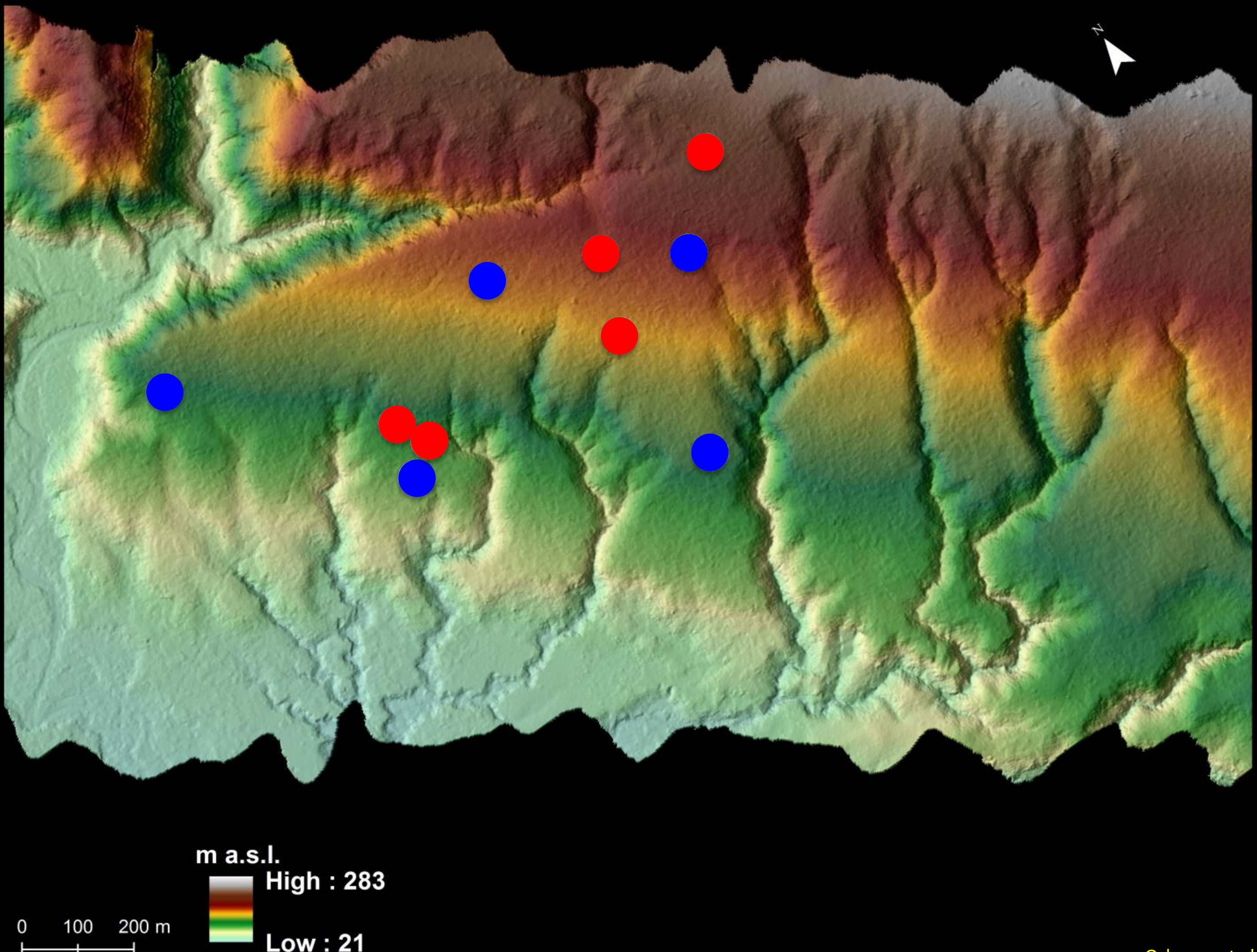
Osborne et al, in revision

Organisms



Osborne et al, in revision

Organisms



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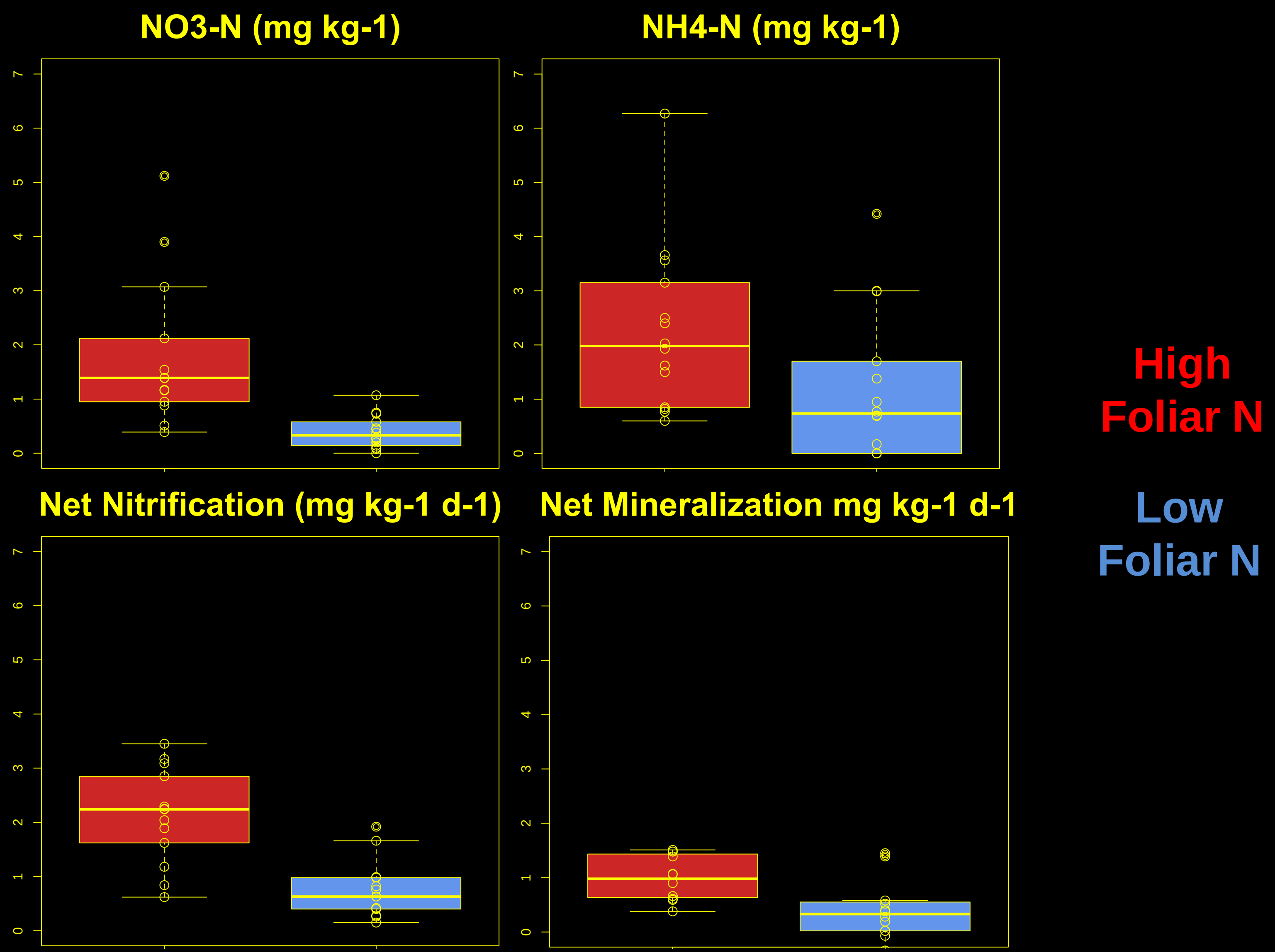
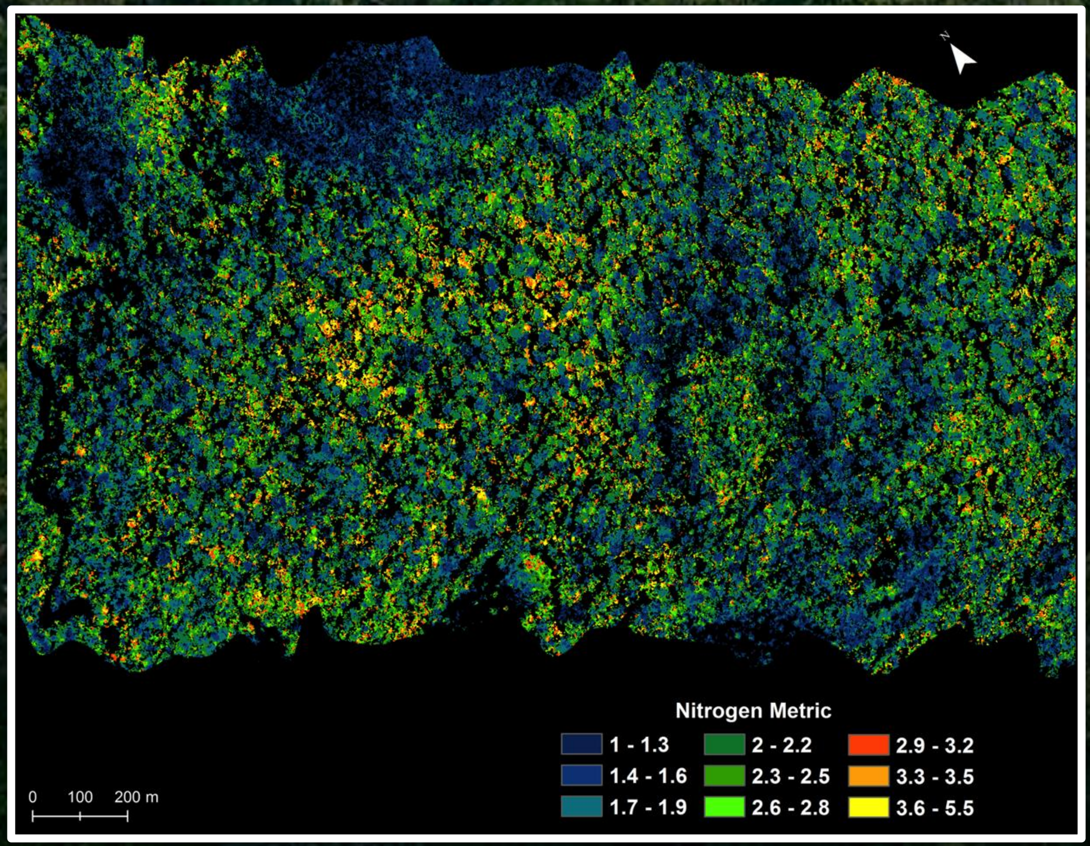
Organisms – link to soil N



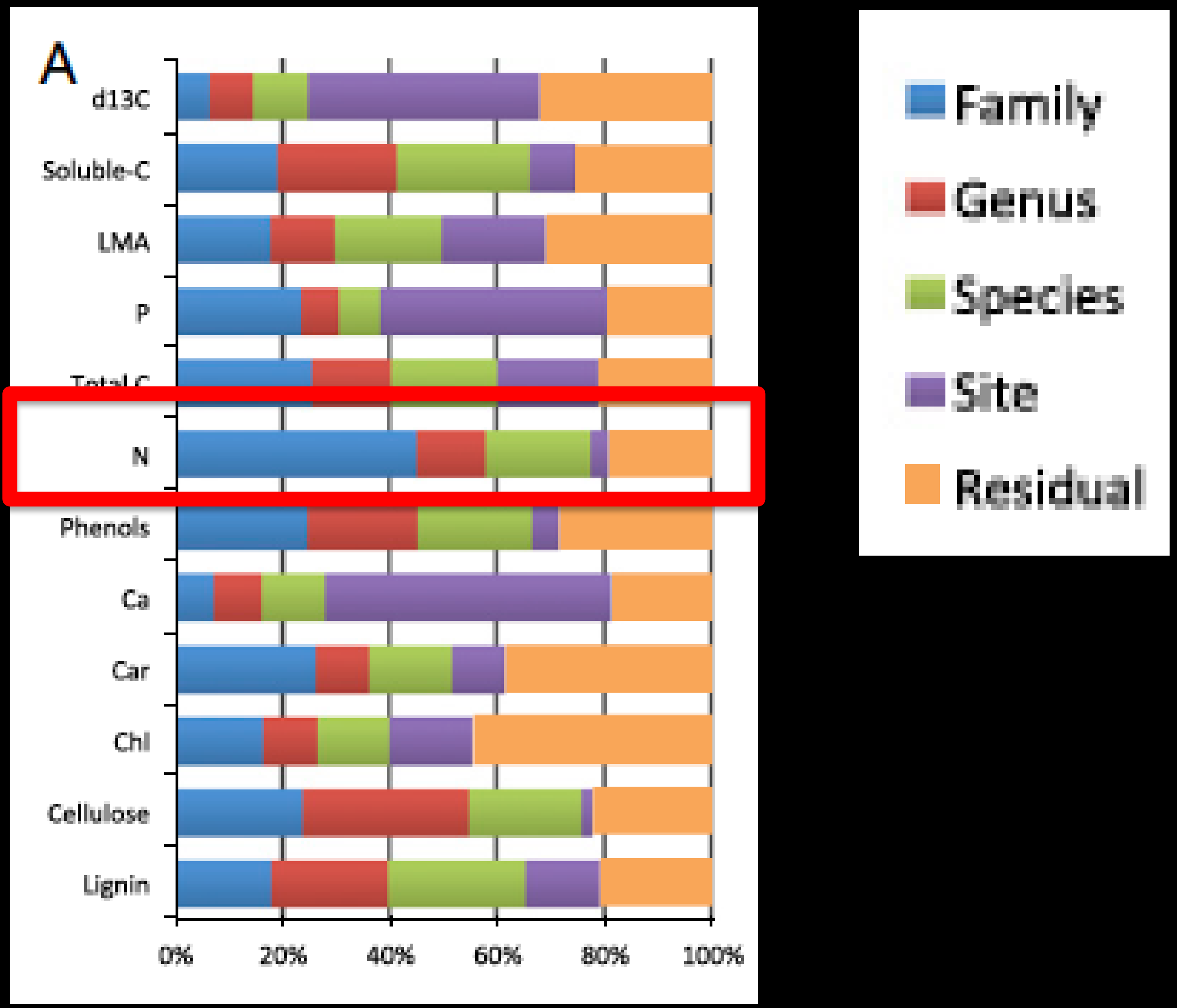
Osborne et al, in revision

Airborne mapping may help deal with heterogeneity at large scales



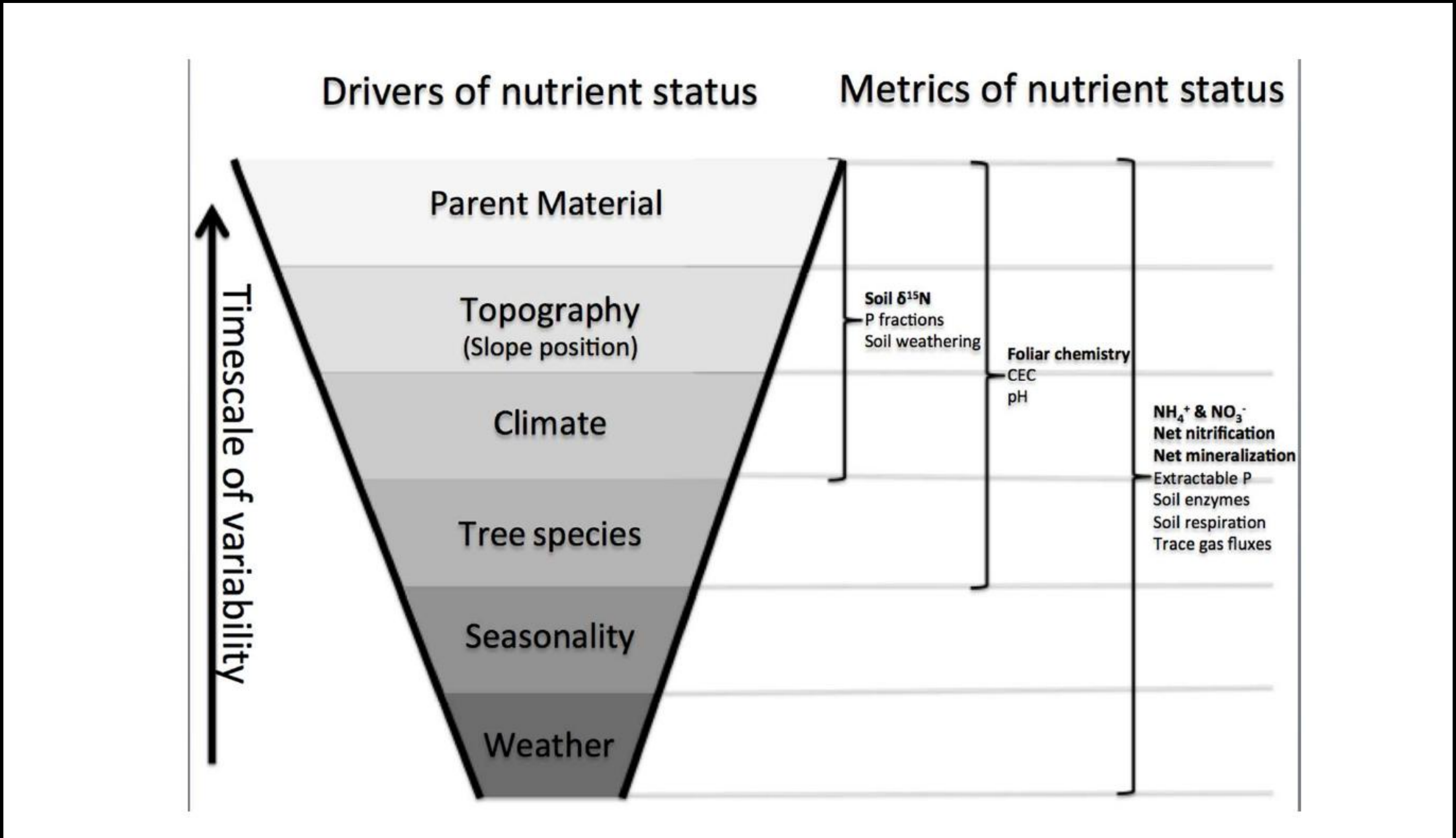
Osborne et al, in revision

The role of trees in driving the N cycling may be more important than we know.



Asner et al., 2014

“The tropics” are not one place!!!



Osborne et al, in revision

Questions?