Ecosystem element cycling can be driven by an organism's need for growth, or by an organism's need for energy.

N cycling:

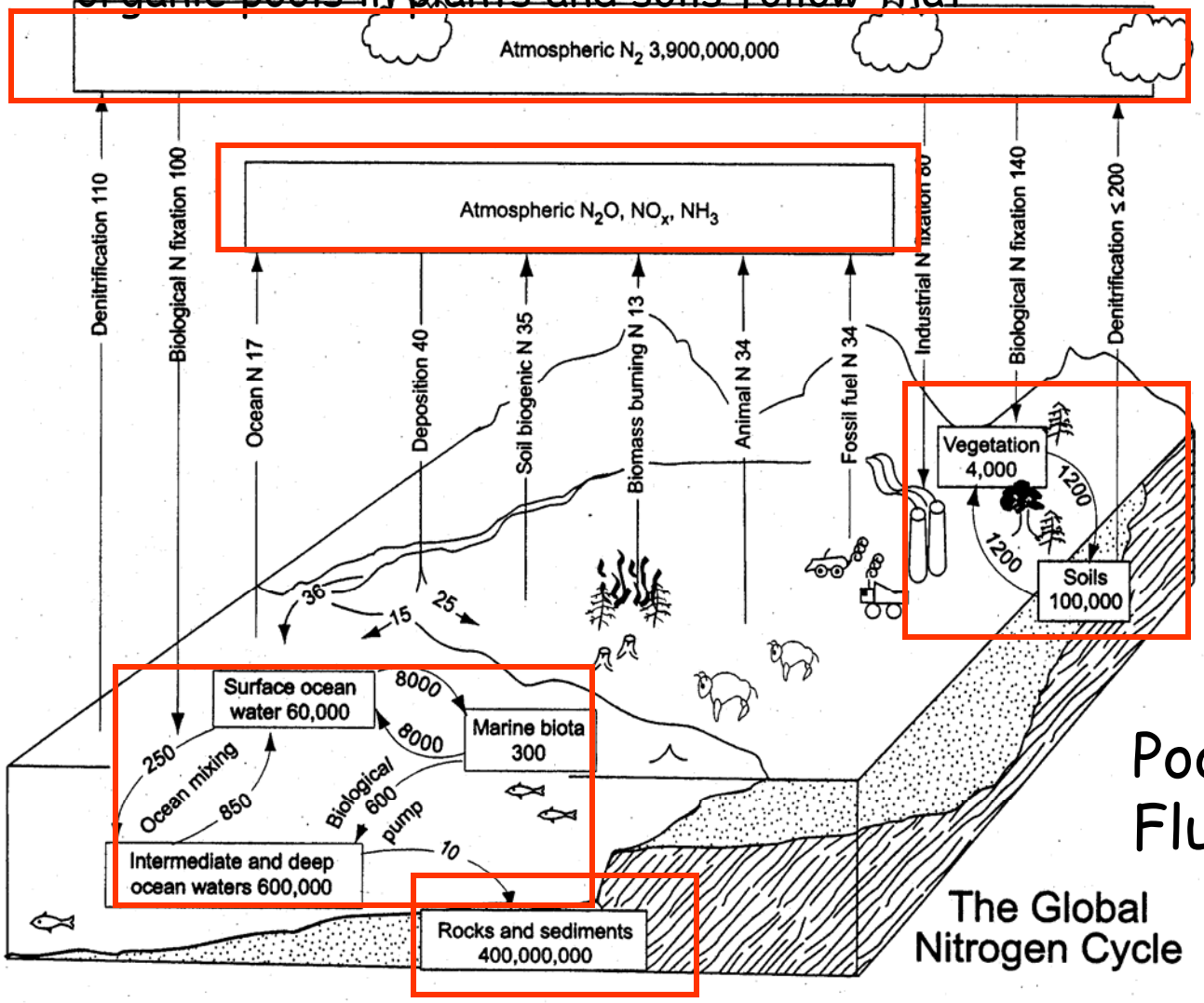
-Nitrogen is essential for life

-Necessary for growth, e.g. synthesis of nucleic acids, proteins

-N_2 comprises 78% of the atmosphere; yet it is limiting - most life forms cannot use it directly from the atmosphere

Global Pools of N:

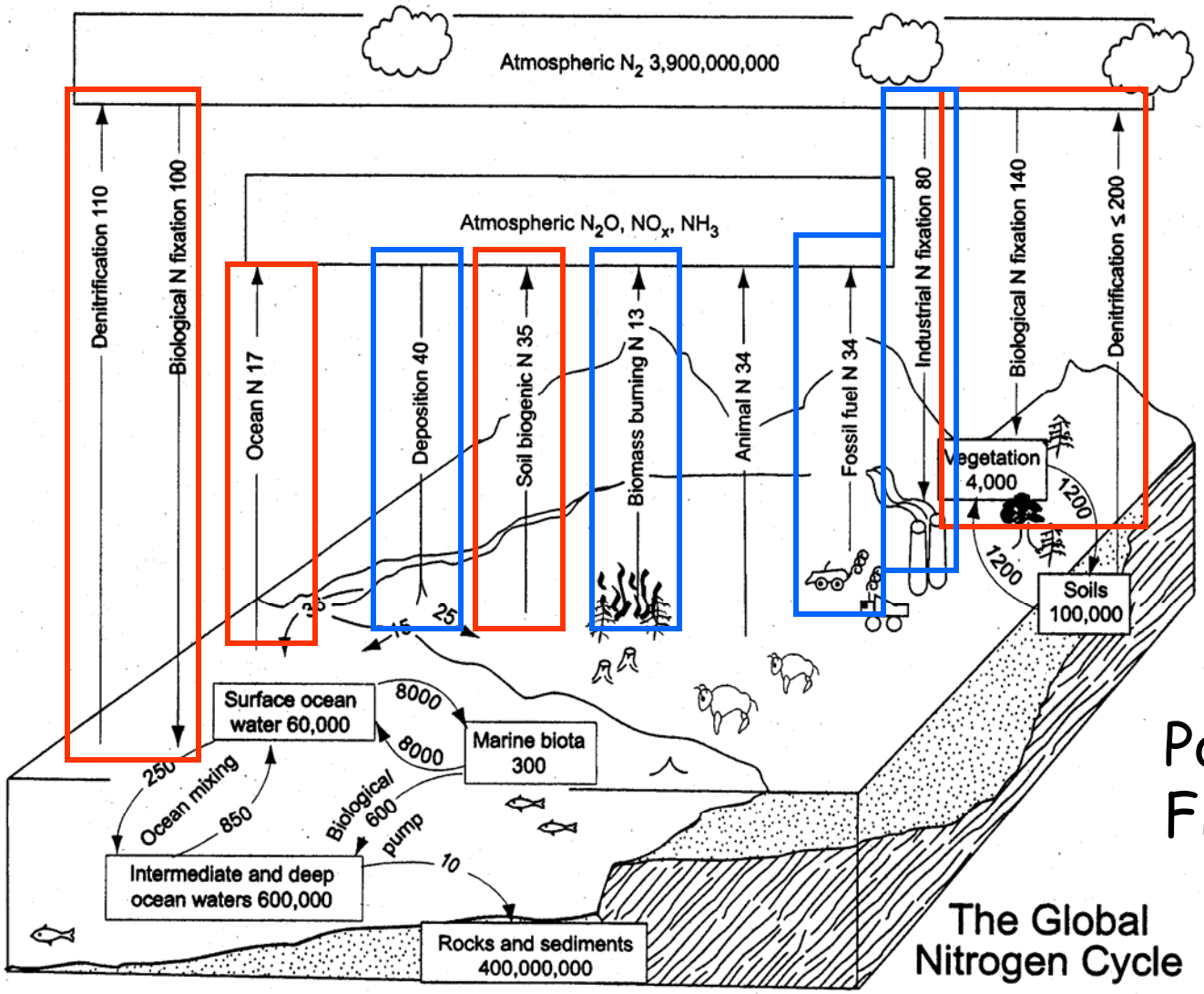
- most in the atmosphere, but not biologically available
- reactive N in atmosphere: trace gases
- lots in sediments and rocks , but not available
- inorganic N in ocean is next largest
- organic pools in plants and soils follow that



Pools in Tg = 10^{12} g
Fluxes in Tg yr^{-1}

Fluxes between biosphere-atmosphere:

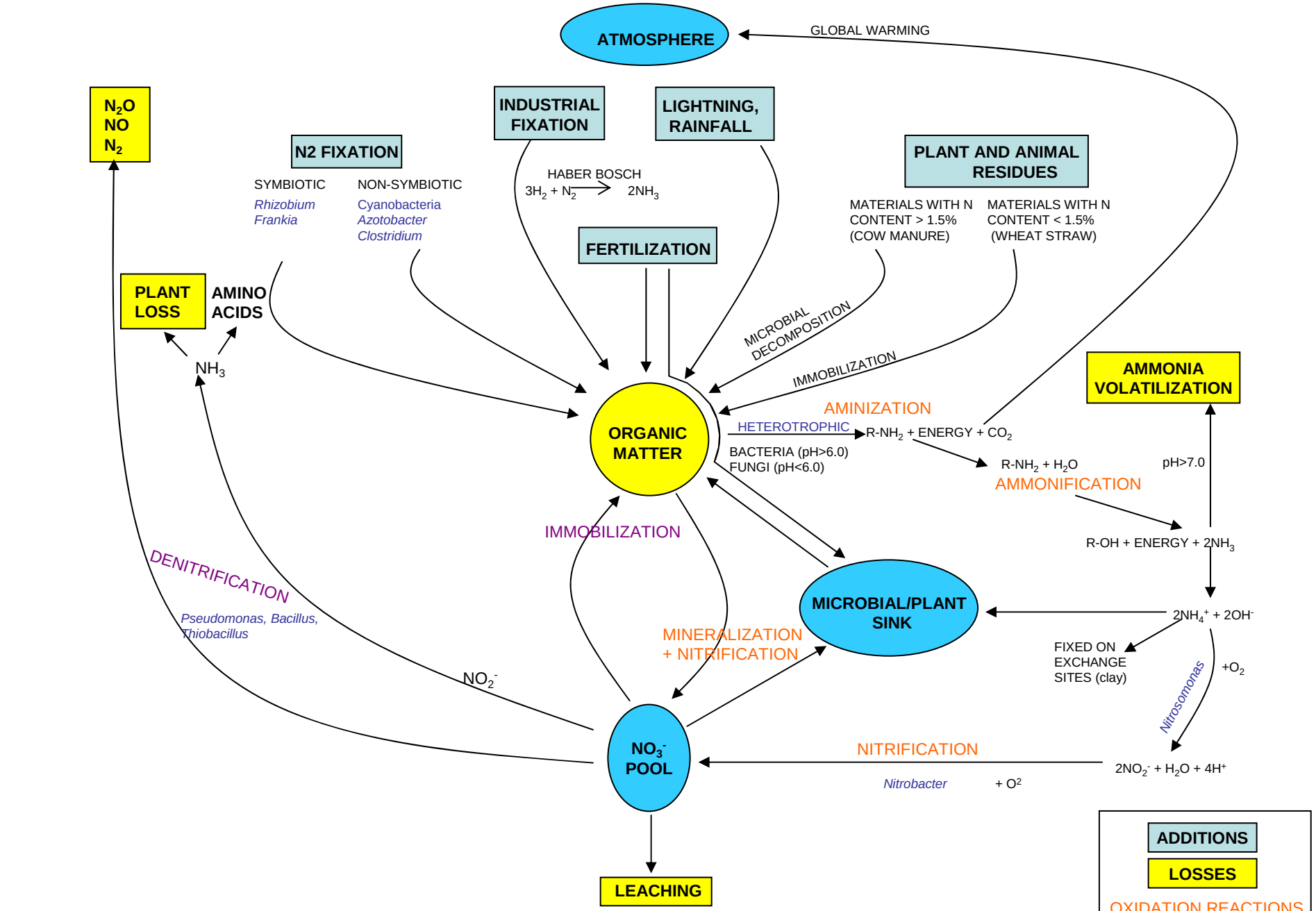
- biological: fixation, denitrification, nitrification
- abiotic: industrial fixation, lightning fixation, fossil fuel and biomass burning, deposition



The Global Nitrogen Cycle

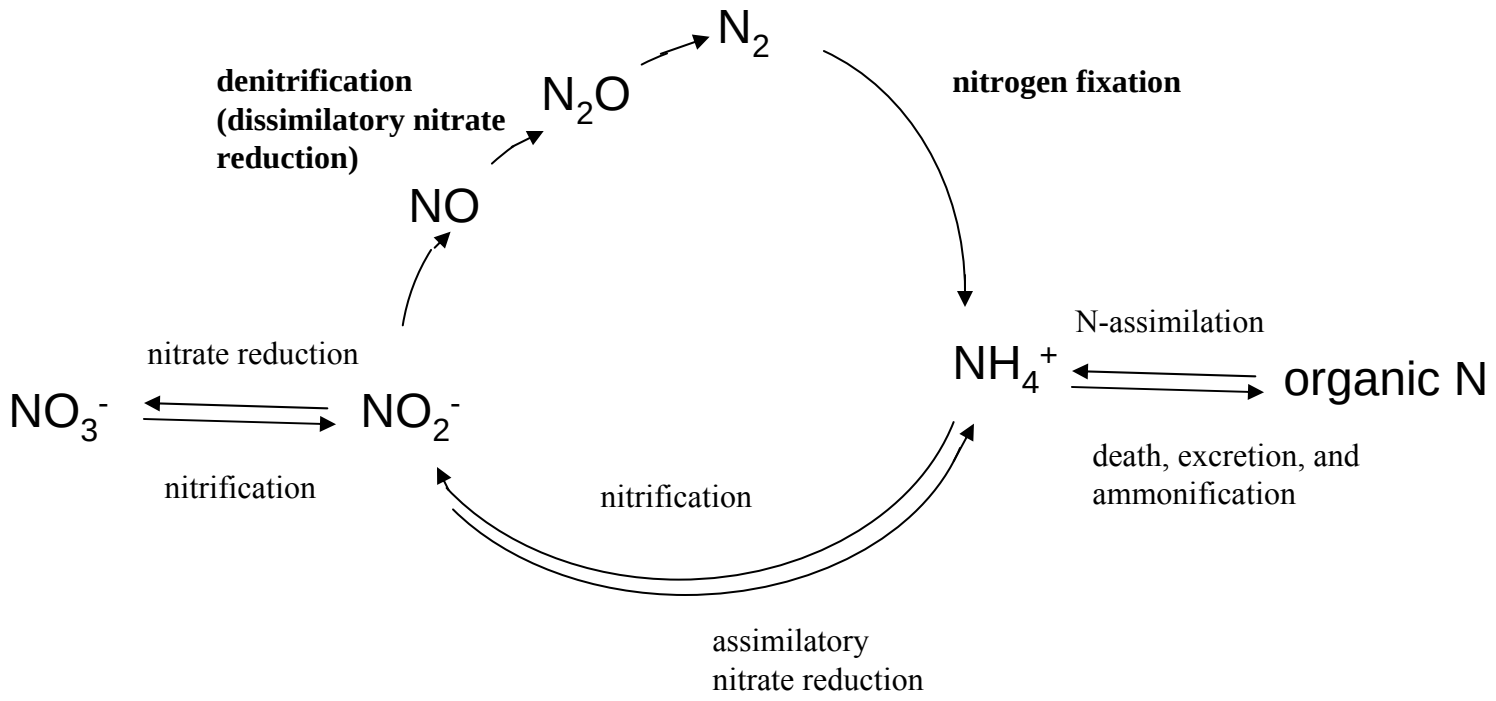
Pools in Tg
Fluxes in Tg yr^{-1}

Comprehensive biotic/abiotic N cycle



Adapted from: LaRuffa, Mullen, Thomason, Mullins, Taylor, and Lees, Oklahoma State University

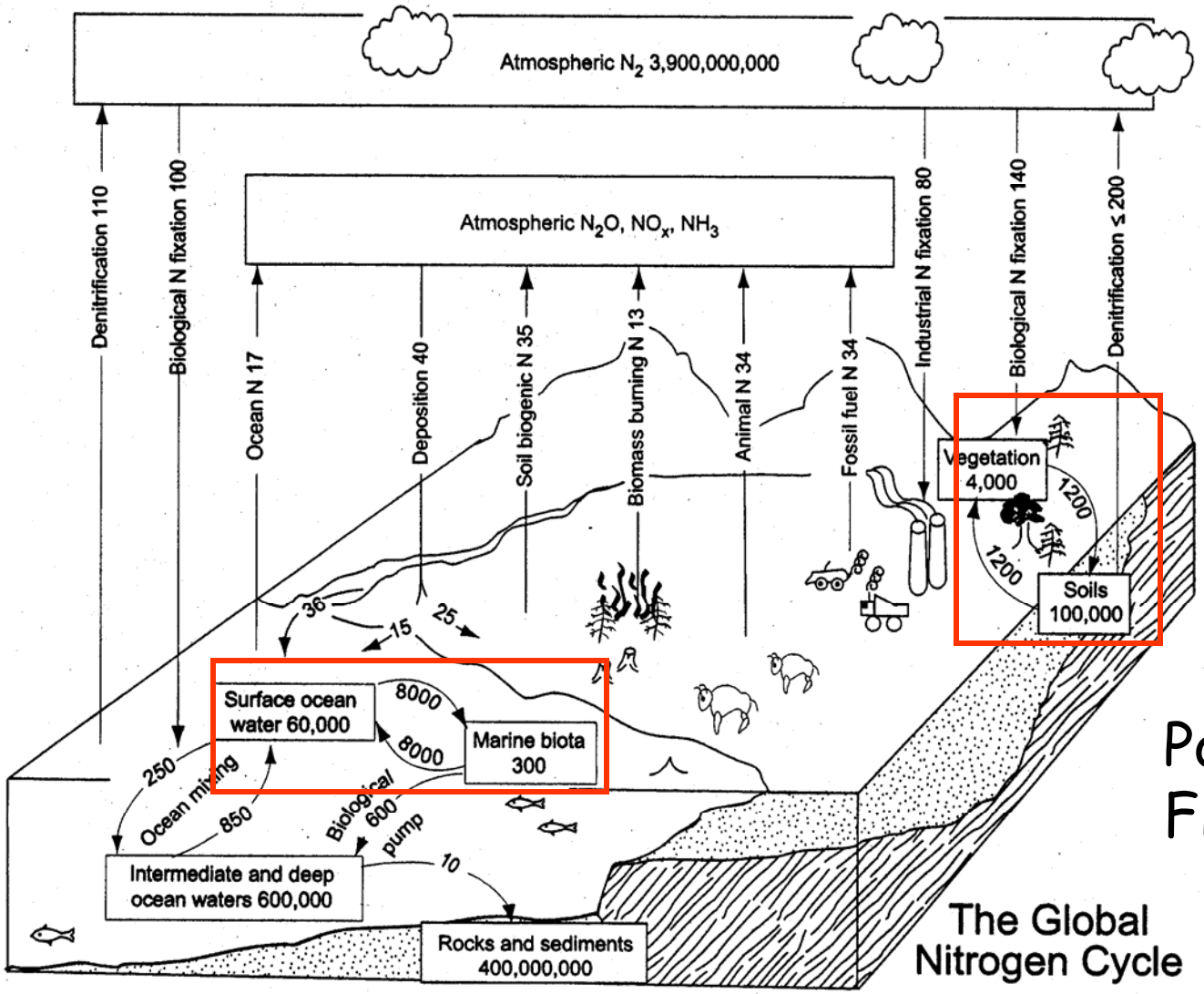
Microbial enzymatic processes drive <u>biological</u> N cycle



Nutrient cycles are not necessarily continuous in space or time

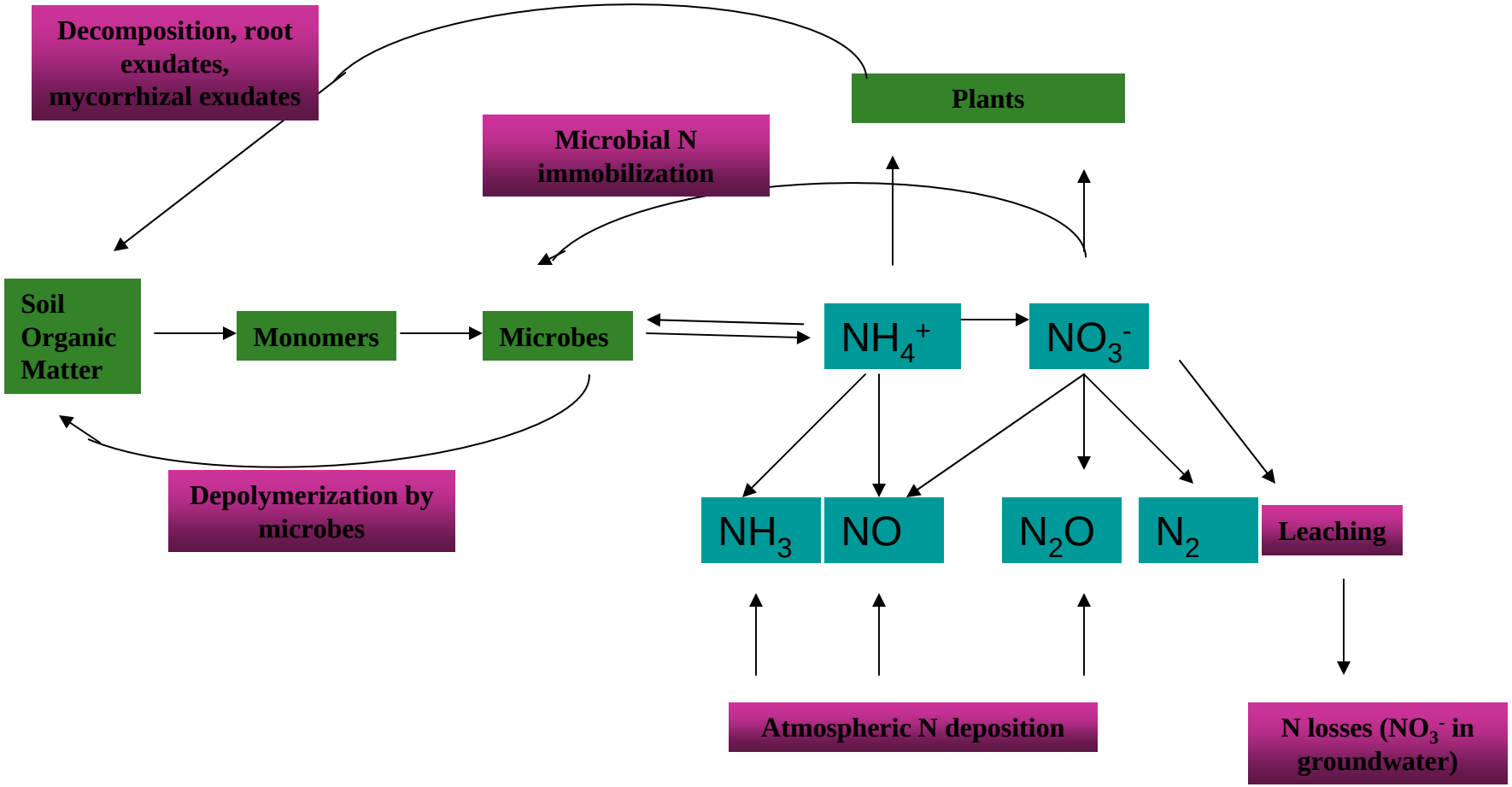
Nutrient cycle processes do not evolve to "help" the ecosystem – they are selected by survival of organisms within niches.

Biological cycling within systems greatly outweighs inputs/outputs – not very "open"



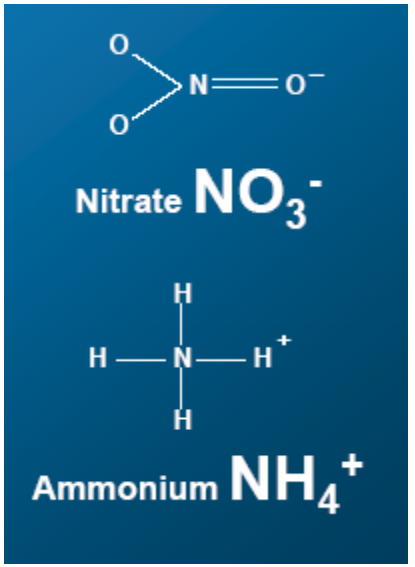
Pools in Tg
Fluxes in Tg yr^{-1}

The Soil N Cycle: microbes are central to turnover



NO_3^- and NH_4^+ are used by plants and microbes for protein synthesis.

Plants have high-affinity transporters for NO_3^- and NH_4^+
Ammonium preferred; nitrate subject to leaching in runoff



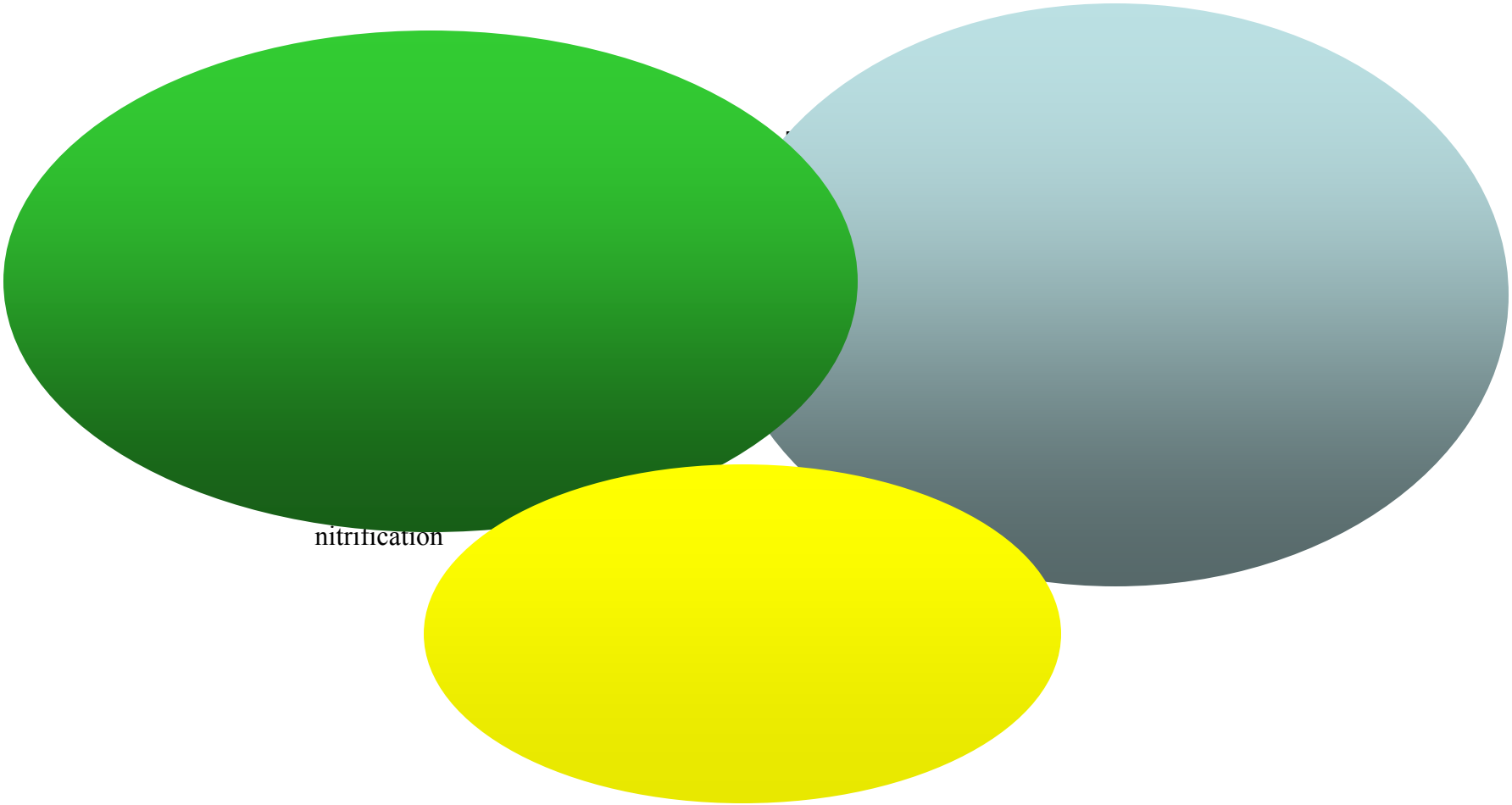
NO, N_2O, N_2 are gases that are lost from ecosystems to the atmosphere

Nitrous oxide (N_2O = depletes ozone; greenhouse gas, 4th behind CO2 because of longevity, stable)

Nitric oxide (NO) – interacts with organic compounds to form ozone, nitric acid if mixed with rain, unstable, free radical

At high pH (>8), NH_3 can also escape as gas

Balance among major processes determines net N available in ecosystem



Nitrogen fixation is the chemical transformation of N_2 to NH_3

Industrial: Haber-Bosch process used to make fertilizer and explosives.

$$N_2 + 3H_2 \rightarrow 2NH_3 \qquad -16.6 \text{ kJ/mol}$$

Exergonic but lacks catalyst to proceed spontaneously at RT
Industrial: 400°C-600°C; 100-200 atm.

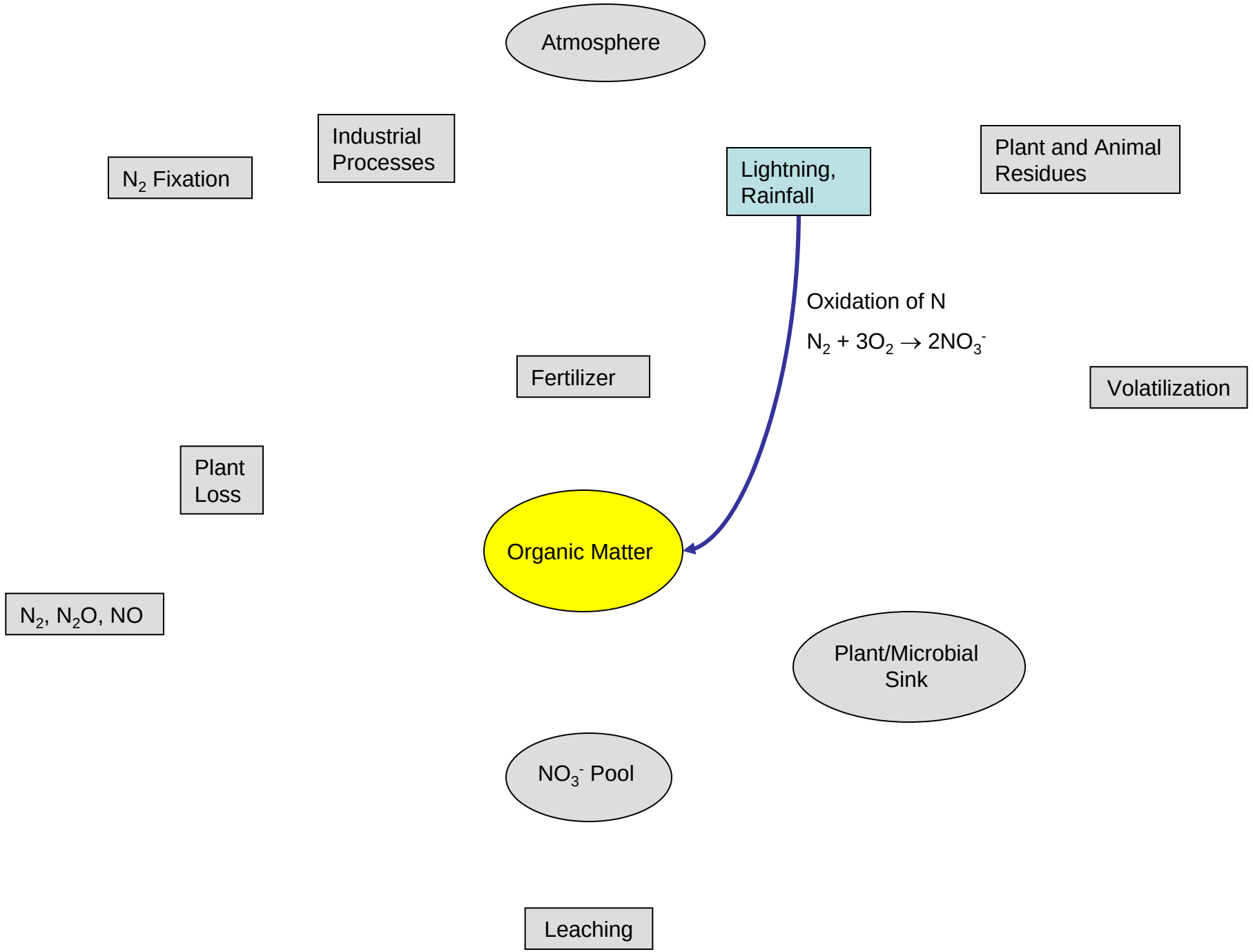
Biological: mutualistic relationship between legumes and *Rhizobium* or related genera; OR done by free living Bacteria and Archaea (e.g. *Azotobacter*).

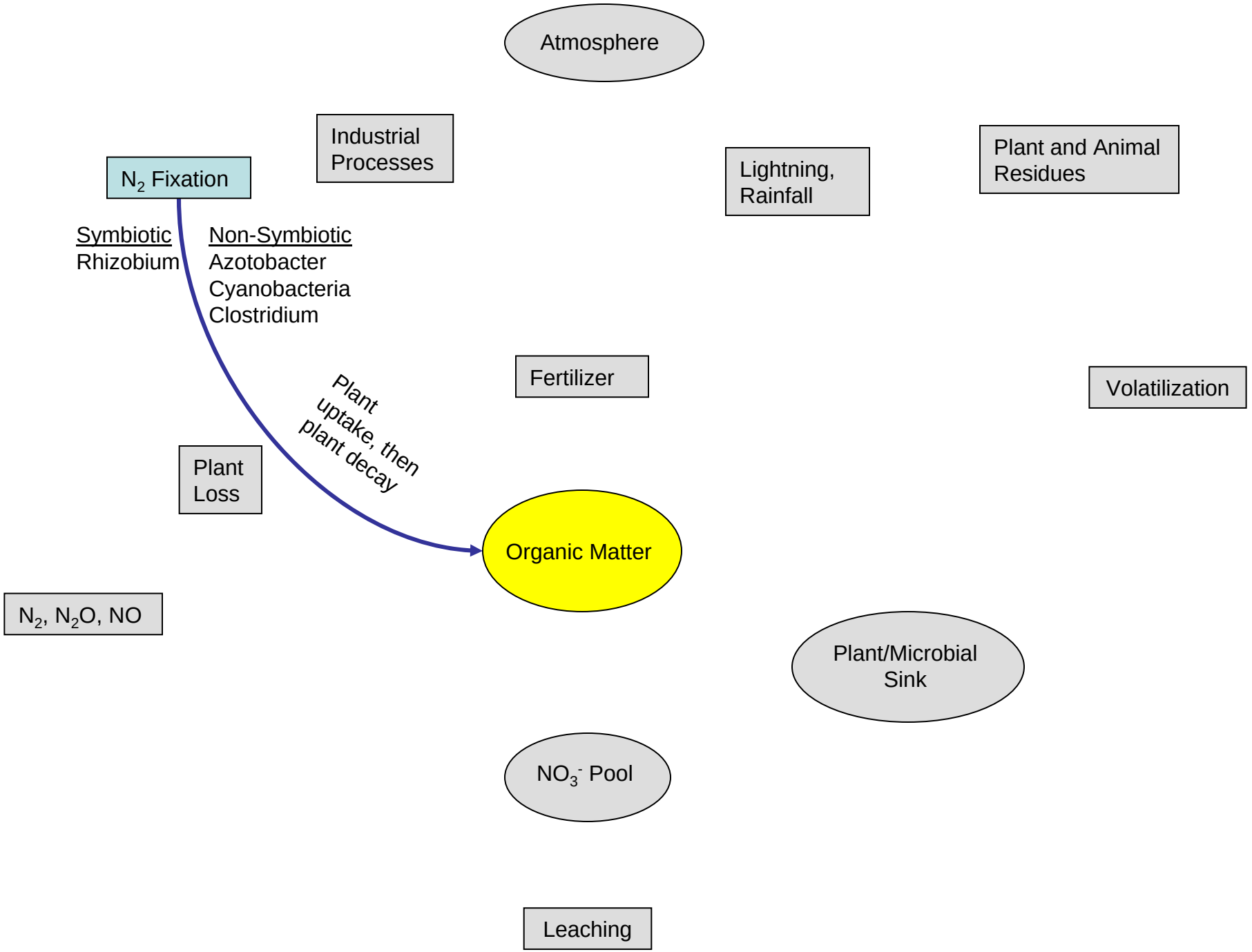
$$N_2 + 10H^+ + 8e^- \rightarrow 2NH_4^+ + H_2$$

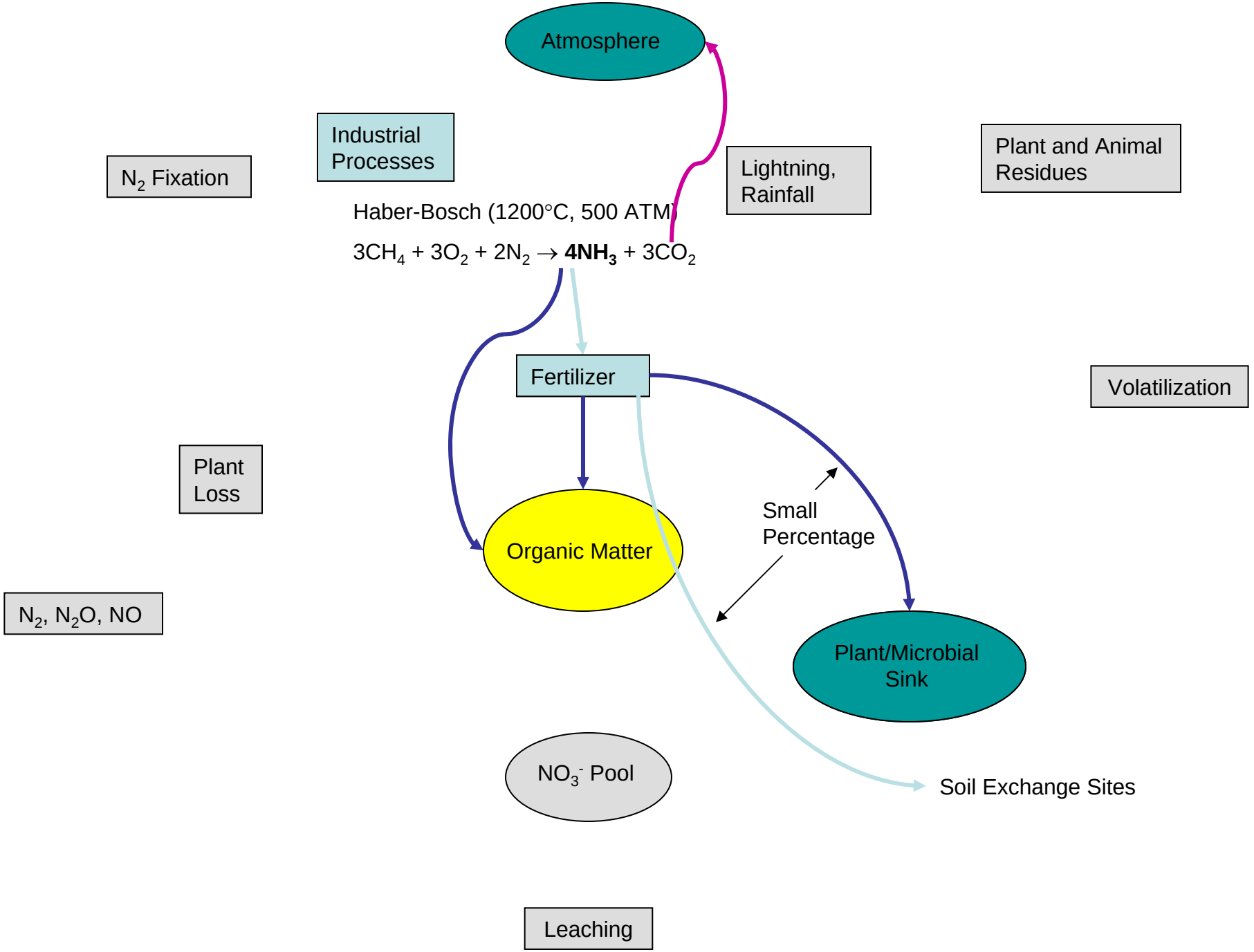
Also exergonic, but requires input of 16 ATP per molecule of N_2 reduced.
Requires e^- source. H_2 is "by-product"
… *in what way might this be useful to humans*??

Combustion of fossil fuels: combustion engines and thermal power plants release various nitrogen oxides (NO_x).

Other processes: formation of NO from N_2 and O_2 due to photons and lightning are important for atmospheric chemistry, although minor contributors to terrestrial or aquatic N pools.


Atmosphere
Industrial Processes
N_2 Fixation
Lightning, Rainfall
Plant and Animal Residues
Oxidation of N
$N_2 + 3O_2 \rightarrow 2NO_3^-$
Fertilizer
Volatilization
Plant Loss
Organic Matter
N_2, N_2O, NO
Plant/Microbial Sink
NO_3^- Pool
Leaching


Atmosphere
Industrial Processes
Lightning, Rainfall
Plant and Animal Residues
N_2 Fixation
Symbiotic
Rhizobium
Non-Symbiotic
Azotobacter
Cyanobacteria
Clostridium
Fertilizer
Volatilization
Plant uptake, then plant decay
Plant Loss
Organic Matter
N_2, N_2O, NO
Plant/Microbial Sink
NO_3^- Pool
Leaching


Atmosphere
Industrial Processes
N_2 Fixation
Lightning, Rainfall
Plant and Animal Residues
Haber-Bosch (1200°C, 500 ATM)
$3CH_4 + 3O_2 + 2N_2 \rightarrow \mathbf{4NH_3} + 3CO_2$
Fertilizer
Volatilization
Plant Loss
Organic Matter
Small Percentage
N_2, N_2O, NO
Plant/Microbial Sink
NO_3^- Pool
Soil Exchange Sites
Leaching

Nodules on plant roots

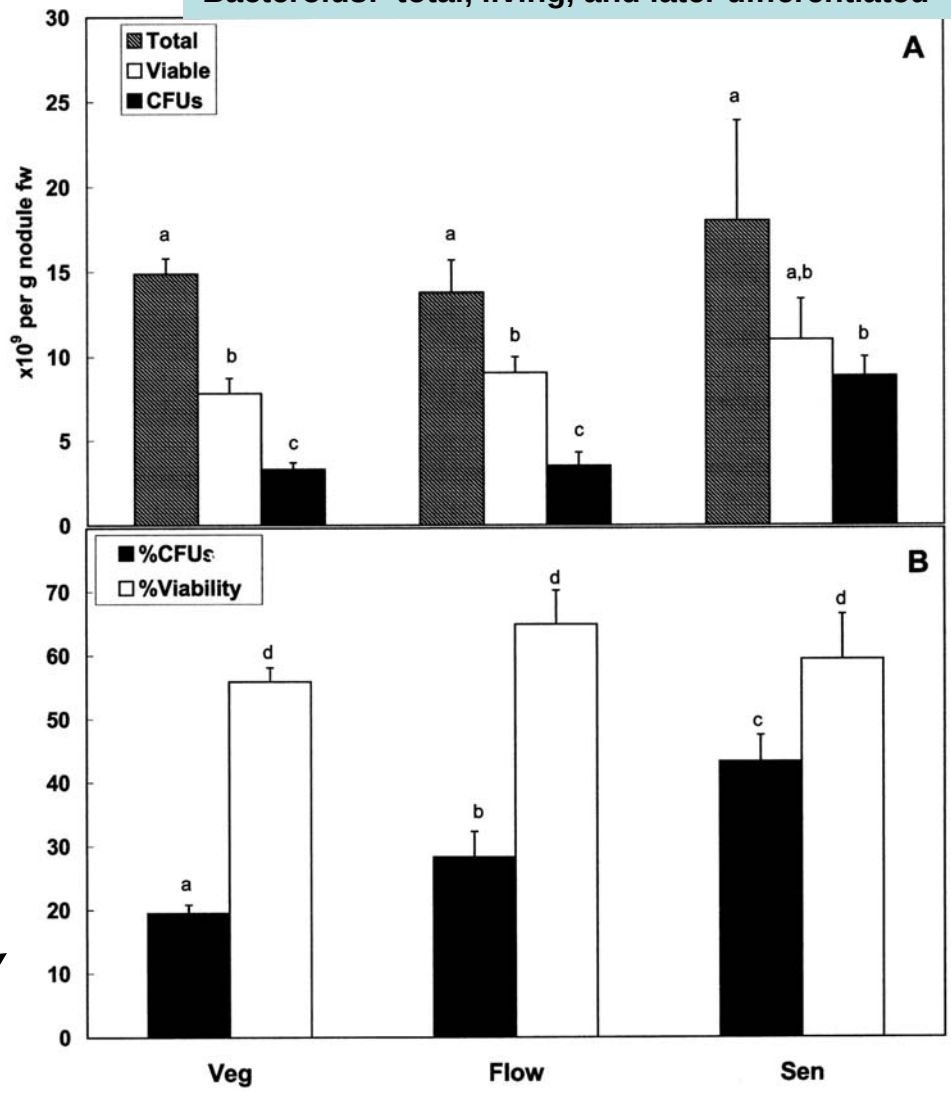
Mutualism… really??

Senescing bacteroids have potential to re-differentiate into free-living rhizobia

Number of bacteroids in *L. japonicus* root nodules and their potential to redifferentiate into growing bacteria, grouped according to the developmental status of the plant.

L. japonicus was inoculated with *Rhizobium*, grown 11 weeks, and grown in darkness 1 week (senescence induction)

Bacteroids: total, living, and later differentiated



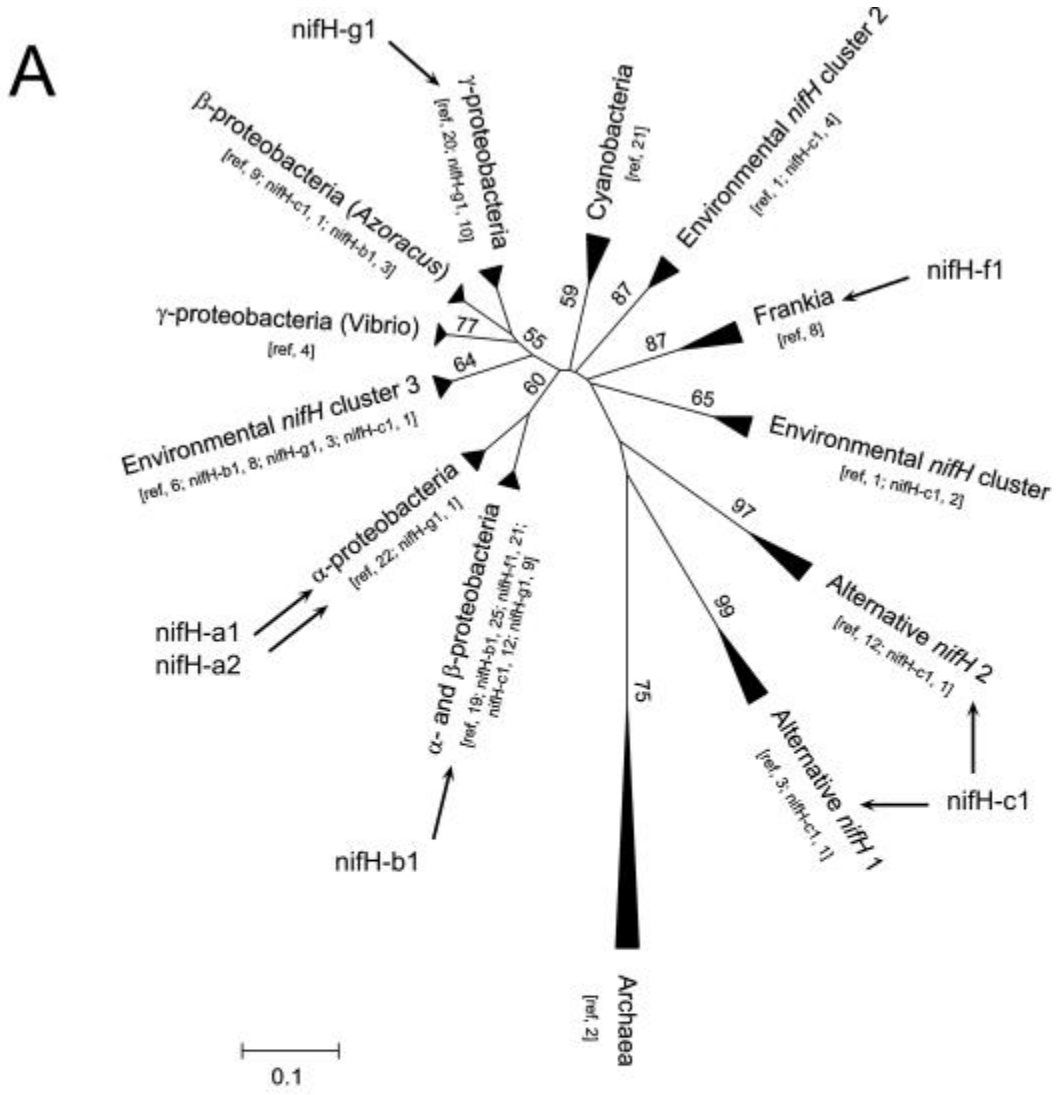
% total bacteroids living and later differentiated

Müller et al. 2001. J. Exp. Bot. 52: 2181

Free-living diazotrophs

Autotrophs, heterotrophs, anaerobes, aerobes, facultatives.

CFUs per gram of soil in different crop rhizospheres varied from 1×10^4 to 8×10^5.



Bürgmann et al., 2004. Appl. Env. Microbiol. 70: 240.

Nitrogenase:

-3 main types
Molybdenum, vanadium, or iron cofactors

Limitations: cold, O_2, limiting cofactors Fe, P (ATP) or Mo

Gets around O_2 toxicity by day/night (non-cyst forming cyanos), crowding, symbiosis, compartmentalization (cyst cyanos)

Found widely: invertebrate guts, soils, plants, bioreactors, lakes, rivers, and the open ocean

But highly conserved: early origin (then retention and loss), or HGT??

nifH has become one of the largest non-ribosomal gene datasets on uncultivated microorganisms

Not likely via HGT – phylogenies align fairly well with 16S so far

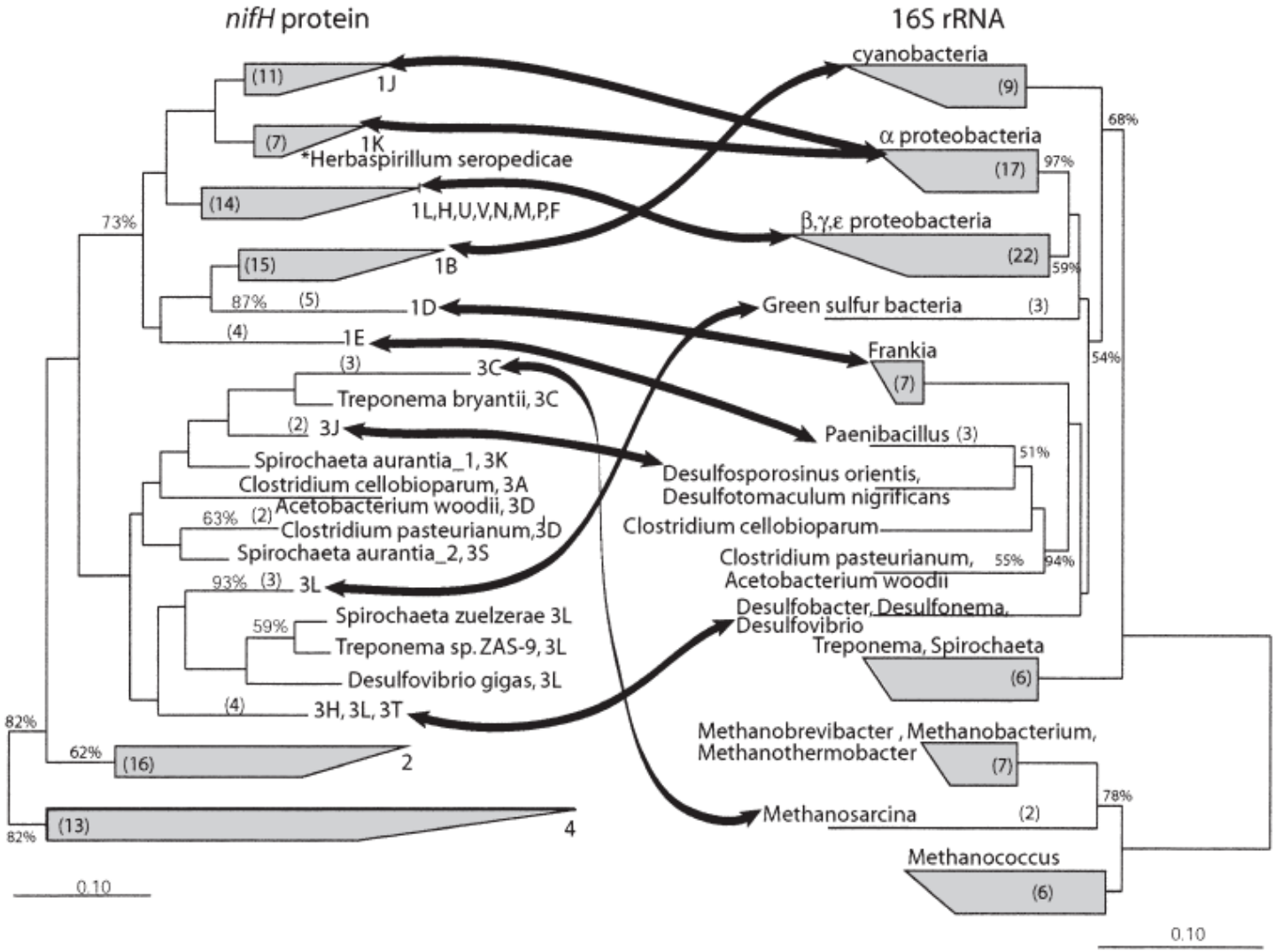


Fig. 3. Comparison of *nifH* (A) and 16S rRNA (B) phylogeny for cultivated microorganisms. *nifH* and 16S rRNA sequences were aligned and analysed by neighbour-joining using ARB. Analysis was bootstrapped and bootstrap values greater than 50% are indicated at respective nodes. Numbers in brackets indicate number of sequences in each cluster. *nifH* cluster names refer to cluster designations shown in Figs 1 and 2.

Zehr et al., 2003. Env. Microbiol. 5: 539

Pathways that use N

Assimilatory: incorporation into organic molecules

Most microbes can take up nitrate and incorporate into organic molecules

$NO_3^- + 8\ e^- \rightarrow NH_3$ (nitrate reductase, nitrite reductase)

NH_3 incorporated into glutamine (glutamine synthetase)

Glutamine is the amino donor for purine, pyrimidine, amino sugars and glutamate

Glutamate is the amino donor for amino acid synthesis

Dissimilatory: electron acceptor (respiration; redox balance)

Oxidative: electron source

Pathways that use N

Assimilatory: incorporation into organic molecules

Oxidative: electron source

Dissimilatory: electron acceptor (respiration; redox balance)

a.k.a denitrification

Many microbes, e.g. *Alcaligenes, Pseudomonas, Bacillus, Thiobacillus, Paracococcus*

$NO_3^- + e^- \rightarrow NO_2^-, NO, N_2O, N_2, NH_3$

Membrane-associated enzymes

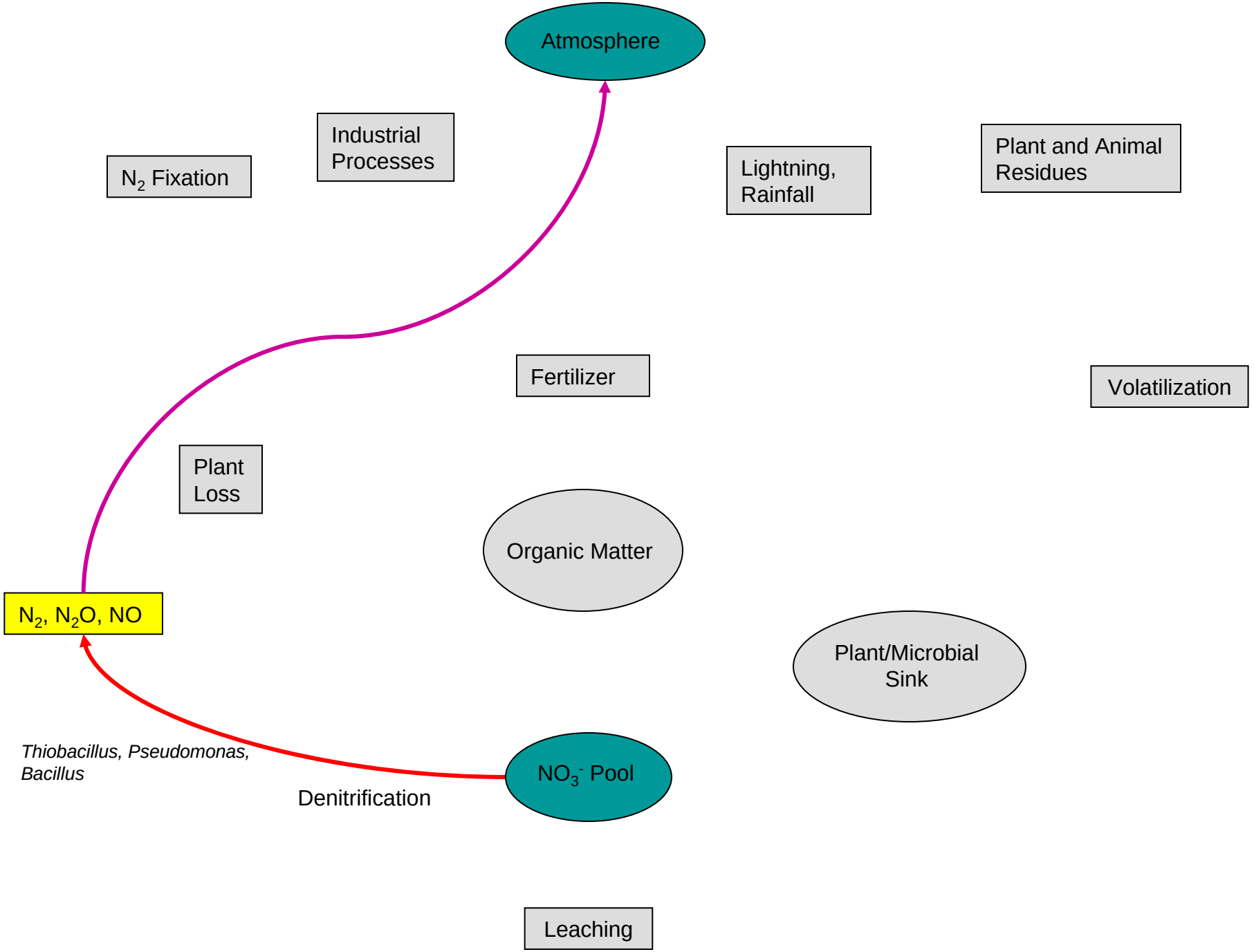
Usually facultative, occurs as substitute for aerobic respiration when O_2 low

Sites of anoxia: waterlogged soils, composting, sludge digestion

Denitrification is the reduction of NO_3^- to nitric oxide (NO), to nitrous oxide (N_2O), and finally to molecular nitrogen (N_2)

$$NO_3^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$$

Denitrification occurs when oxygen is not present and nitrate acts as an electron acceptor


Atmosphere
N_2 Fixation
Industrial Processes
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Plant and Animal Residues
Fertilizer
Volatilization
Plant Loss
Organic Matter
N_2, N_2O, NO
Plant/Microbial Sink
Thiobacillus, Pseudomonas, Bacillus
NO_3^- Pool
Denitrification
Leaching

Nitrate reduction/denitrification

BUT: nitrate reduction can be dissimilatory OR assimilatory.

Separate genes, enzymes for each process; different enzyme localization

Cytoplasmic assimilatory (Nas): requires ABC transport protein to get NO_3^- into cell

Membrane-bound respiratory (Nar) - generates a transmembrane proton motive force (PMF) allowing ATP synthesis

Periplasmic dissimilatory (Nap) nitrate reductases: redox balance (excess reductant)

All systems – highly regulated gene expression

TABLE 1. Prokaryotic nitrate reduction

Characteristic	Assimilatory, NO_3^- assimilation	Dissimilatory	
		NO_3^- respiration	NO_3^- reduction
Nitrate reductase	Assimilatory Nas	Respiratory Nar	Dissimilatory Nap
Location	Cytoplasm	Membrane	Periplasm
Reaction catalyzed	$NO_3^- \Rightarrow NO_2^-$	$NO_3^- \Rightarrow NO_2^-$	$NO_3^- \Rightarrow NO_2^-$
Structural genes	*nasCA*[a]/*narB*[b]	*narGHI*	*napAB*
Prosthetic groups	FAD[c], FeS[d], MGD	cyt*b*[e], FeS, MGD	cyt*c*, FeS, MGD
Nitrate transport	Yes	Yes	No
Function	Biosynthesis of N compounds	PMF (nitrate respiration and denitrification)	2H $\downarrow$[f] and denitrification
Regulation[g]			
O_2	No	Yes	No/yes
NH_4^+	Yes	No	No
NO_3^-/NO_2^-	Yes	Yes	No/yes

[a] Following the gene designation in *K. oxytoca* for the NADH-nitrate reductase.
[b] Following the gene designation in cyanobacteria for the ferredoxin-nitrate reductase.
[c] FAD is present in the diaphorase subunit of the NADH-dependent nitrate reductases, but it is absent from the cyanobacterial ferredoxin-nitrate reductase.
[d] FeS, iron-sulfur centers.
[e] cyt*b*, cytochrome *b*.
[f] 2H$\downarrow$, dissipation of reducing power. A PMF can be generated if a proton-translocating complex is involved in the electron transfer, but in most cases, this seems to be insufficient to support ATP synthesis coupled to nitrate reduction.
[g] Some differences in regulation in prokaryotic organisms have been reported.

Moreno-Vivian, 1999. J. Bacteriol. 181: 6573

Nitrate reduction/denitrification

TABLE 2. Prokaryotic nitrite reduction

Characteristic	Assimilatory, NO_2^- assimilation	Dissimilatory		
		NO_2^- respiration		NO_2^- reduction
		Nir	Nrf	
Nitrite reductase	Assimilatory Nas	Respiratory Nir	Respiratory Nrf	Dissimilatory Nir
Location	Cytoplasm	Periplasm	Periplasm	Cytoplasm
Reaction catalyzed	$NO_2^- \Rightarrow NH_4^+$	$NO_2^- \Rightarrow NO$	$NO_2^- \Rightarrow NH_4^+$	$NO_2^- \Rightarrow NH_4^+$
Structural genes	*nasB*[a]/*nirA*[b]	*nirS*/*nirK*	*nrfA*	*nirBD*
Prosthetic groups	FAD[c], FeS[d], siroheme	cytcd_1[e]/Cu	cytc	FAD, FeS, siroheme
Nitrite transport	Yes	No	No	Yes
Function	Biosynthesis of N compounds	PMF (denitrification)	PMF (ammonification)	2H $\downarrow$[f] and nitrite detoxification
Regulation[g]				
O_2	No	Yes	Yes	Yes
NH_4^+	Yes	No	No	No
NO_3^-/NO_2^-	Yes	Yes	Yes	Yes

[a] Following the gene designation in *K. oxytoca* for the NADH-nitrite reductase.
[b] Following the gene designation in cyanobacteria for the ferredoxin-nitrite reductase.
[c] FAD is present in the NADH-nitrite reductases, but it is absent from the cyanobacterial assimilatory ferredoxin-dependent nitrite reductase.
[d] FeS, iron-sulfur centers.
[e] cytcd_1, cytochrome cd_1 complex.
[f] 2H $\downarrow$, dissipation of reducing power.
[g] Some differences in regulation in prokaryotic organisms have been reported.

Moreno-Vivian, 1999. J. Bacteriol. 181: 6573

Pathways that use N

Assimilatory: incorporation into organic molecules
Dissimilatory: electron acceptor (respiration; redox balance)

Oxidative: electron source

Ammonia-oxidizing bacteria and nitrite-oxidizing bacteria
a.k.a. nitrifiers ➔ aerobic, obligate chemolithoautotrophs (except *Nitrobacter* – facultative)
NH_3 from denitrification diffuses from anoxic niche to **aerobic** niche
Nitrifiers often found at oxic/anoxic boundary

Oxidation under anoxic conditions: an oxymoron?
anammox: $NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O$

Nitrification is the oxidation of ammonium:

ammonium (NH_4^+) to nitrite (NO_2^-)
nitrite (NO_2^-) to nitrate (NO_3^-)

Sources of ammonia:

Nitrogen fixation
Nitrate reduction
Ammonification (conversion of organics, *e.g.* amino acids, to NH_3)

Nitrification (oxidative N utilization)

Nitrification = 2-step process

1. Ammonia oxidation

Nitrosomonas, Nitrosococcus, Nitrosospira, Nitrosolobus, Nitrosovibrio
(terrestrials = β-proteobacteria; marine = γ-proteobacteria)

1a. ammonia monooxygenase, AMO, cell membrane

$$2H^+ + NH_3 + 2e^- + O_2 \rightarrow NH_2OH + H_2O$$

1b. hydroxylamine oxidoreductase, HAO, periplasm

$$NH_2OH + H_2O \rightarrow HONO + 4\ e^- + 4H^+$$

4 e^- to electron transport chain; sole source of energy for *Nitrosomonas*

2. Nitrite oxidation

Nitrobacter, Nitrococcus, Nitrospina, Nitrospira

electrons flow from nitrite to oxygen via reversed electron flow in membrane

Old paradigm: **Nitrification** is an **aerobic** process.
NH_3 from denitrification diffuses from anoxic niche to **aerobic** niche
Nitrifiers often found at **oxic/anoxic** boundary

Oxidation under anoxic conditions: an oxymoron?

anammox: $NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O$

Major contribution to cycling inorganic N in oceans
Nitrite can even come from denitrification (dissimilatory nitrate reduction) in same cells

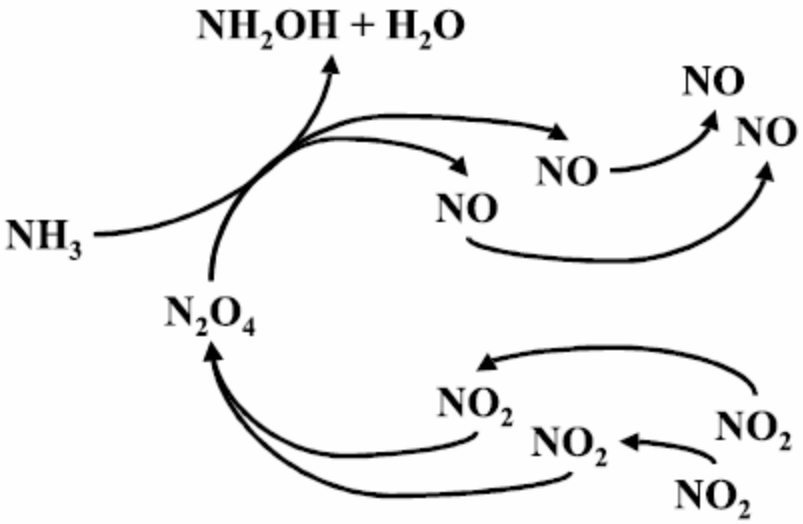
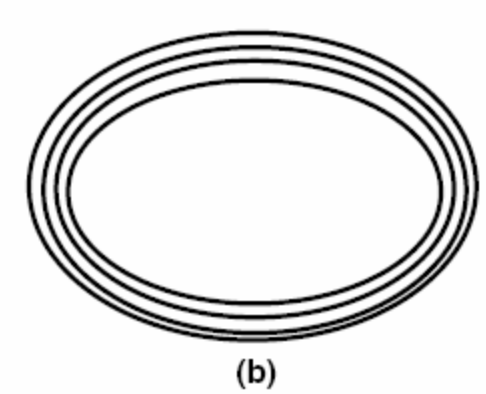


Fig. 3. NO_x cycle. Hypothetical model of the anaerobic NO_2-dependent ammonia oxidation by *Nitrosomonas*. N_2O_4 is the oxidant for the ammonia oxidation.

Schmidt et al., 2001. FEMS Microbiol. Ecol. 39: 175



Anaerobic:
AMO down, membranes up

Niftrik et al., 2004. FEMS Microbiol. Lett. 233: 7

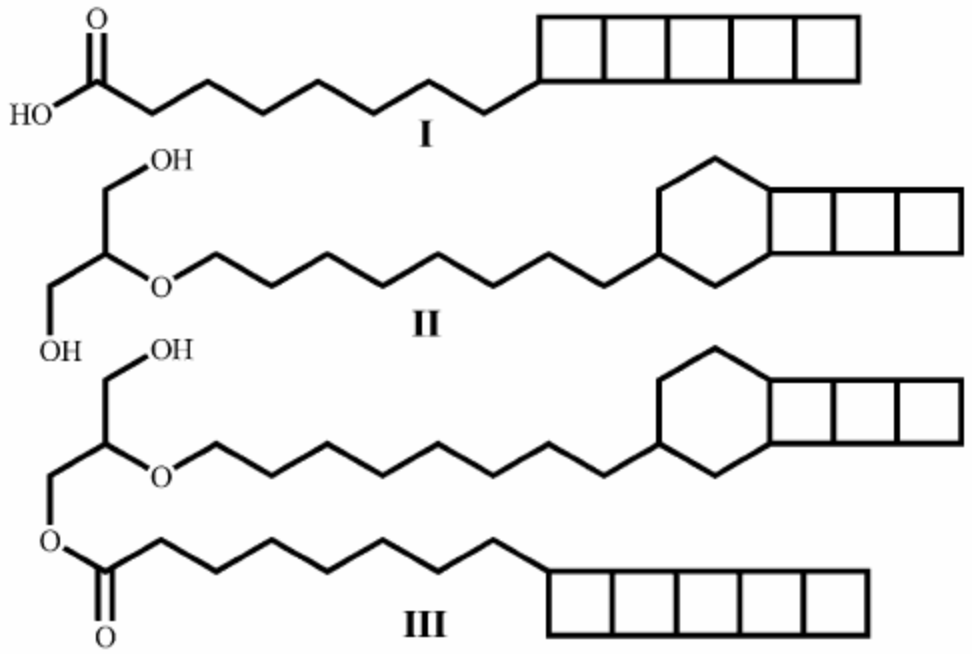


Fig. 3. Structures of three characteristic ladderane lipids: I ladderane fatty acid-containing ring-system Y. II ladderane monoalkyl glycerol ether-containing ring-system X. III ladderane glycerol ether/ester containing both ring-systems, X and Y. Lipids containing ladderane moieties X and Y are abundant membrane lipids in anammox bacteria. Adapted with permission from Jetten et al. [29].

Niftrik et al., 2004. FEMS Microbiol. Lett. 233: 7

Domain Bacteria
Phylum Planctomycetes

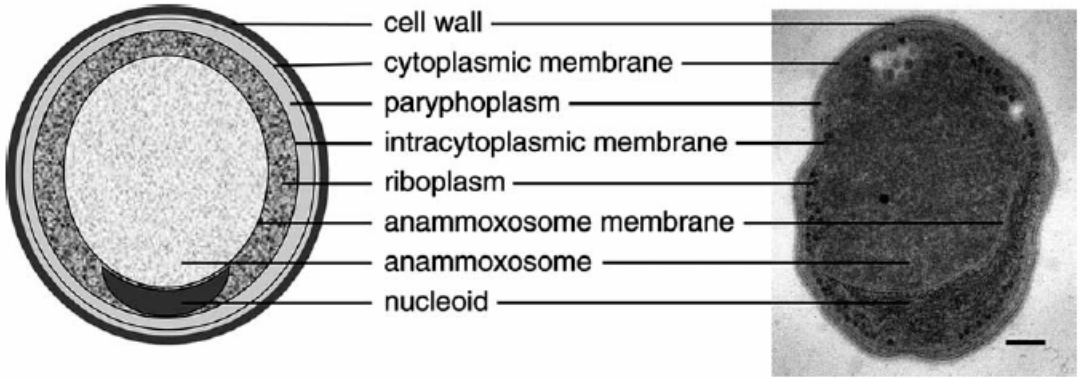


Fig. 2. Cellular compartmentalization in anammox bacteria. Left: schematic drawing, right: thin section of cryosubstituted *Candidatus* "Brocadia anammoxidans" seen via transmission electron microscopy. *Bar* 100 nm.

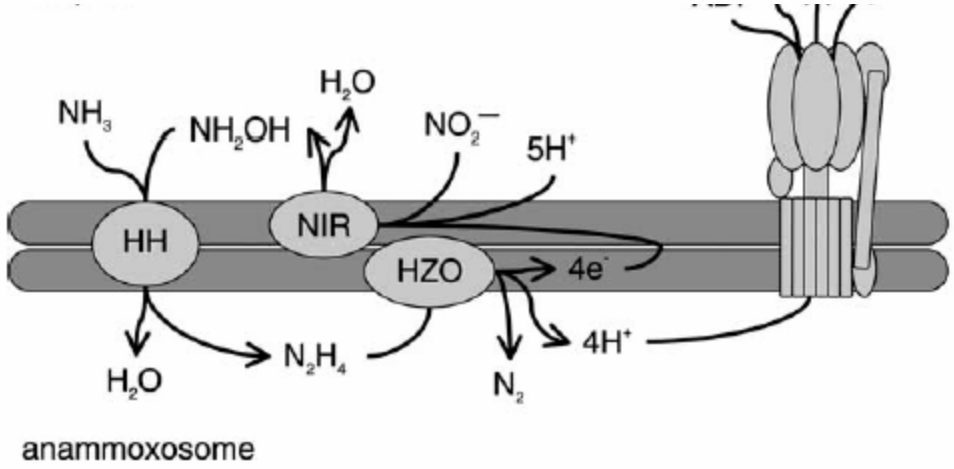


Fig. 4. Postulated anaerobic ammonium oxidation coupled to the anammoxosome membrane in anammox bacteria resulting in a proton motive force and subsequent ATP synthesis via membrane-bound ATPases. HH: hydrazine hydrolase; the hydrazine-forming enzyme, HZO: hydrazine-oxidizing enzyme, NIR: nitrite-reducing enzyme.

Niftrik et al., 2004. FEMS Microbiol. Lett. 233: 7

JOURNAL OF BACTERIOLOGY, May 2003, p. 2759–2773 Vol. 185, No. 9
0021-9193/03/$08.00+0 DOI: 10.1128/JB.185.9.2759–2773.2003

Complete Genome Sequence of the Ammonia-Oxidizing Bacterium and Obligate Chemolithoautotroph *Nitrosomonas europaea*†

Patrick Chain,[1,2] Jane Lamerdin,[1,2] Frank Larimer,[1,3] Warren Regala,[1,2] Victoria Lao,[1,2] Miriam Land,[1,3] Loren Hauser,[1,3] Alan Hooper,[4] Martin Klotz,[5] Jeanette Norton,[6] Luis Sayavedra-Soto,[7] Dave Arciero,[4] Norman Hommes,[7] Mark Whittaker,[4] and Daniel Arp[7]*

Joint Genome Institute, Walnut Creek, California 94598[1]; Lawrence Livermore National Laboratory, Livermore, California 94550[2]; Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831[3]; University of Minnesota, Minneapolis, Minnesota 55455[4]; University of Louisville, Louisville, Kentucky 40208[5]; Utah State University, Logan, Utah 84322[6]; and Oregon State University, Corvallis, Oregon 97331[7]

TABLE 1. Summary of *N. europaea* genome

Parameter	Value
No. of chromosomes	1
No. of bp	2,812,094
GC content (%)	50.7
Coding density (%)	88.4
No. of predicted protein coding genes	2,460
No. of predicted proteins with putative function	1,863
No. of unknown proteins with matches to other proteins of unknown function	285
No. of unknown proteins unique to *N. europaea*	312
No. of predicted RNA coding genes	47
No. of tRNAs	41
No. of 16S-Ala $tRNA_{TGC}$-Ile $tRNA_{GAT}$-23S-5S tRNAs	1
No. of genes in protein category[a]:	
Energy	103
Transport	285
DNA replication	212
Transcription	36
Translation	136
Regulation and signaling	187
Amino acid metabolism	120
Carbohydrate metabolism	55
Nucleotide metabolism	48
Cofactor metabolism	80
Lipid metabolism	48
Secondary metabolites	48
Cellular processes	481
General function	155

[a] Classifications of genes are based on clusters of orthologous genes (COGs).

identities down to 30%, over 80% of the length. The sequence, as well as the results of automatic annotations, is available online (http://genome.ornl.gov/microbial/neur/embl/).

Nucleotide sequence accession number. The sequence of the complete *N. europaea* strain ATCC 19718 is available under EMBL-EBI accession number AL954747.

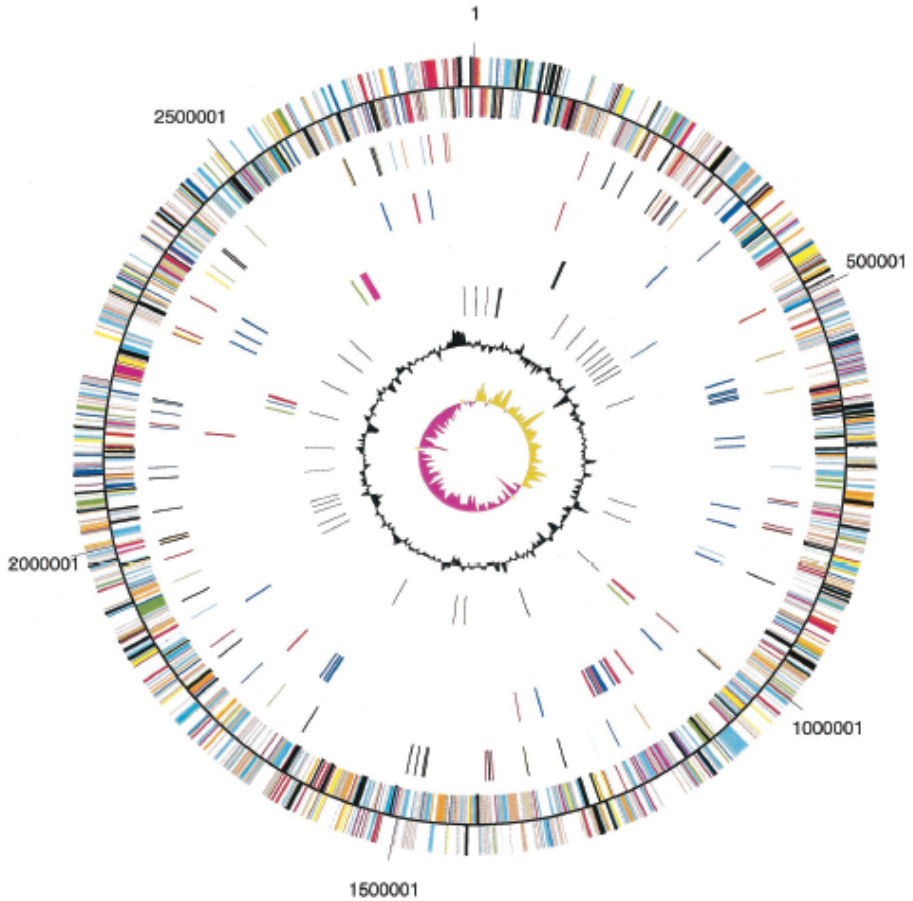


FIG. 1. Circular representation of the 2,812,094-bp genome of *N. europaea* ATCC 19718. The outer two circles represent protein-encoding and structural-RNA genes, plus and minus strand (green, energy metabolism; red, DNA replication; magenta, transcription; yellow, translation; orange, amino acid metabolism; dark blue, carbohydrate metabolism; pale red, nucleotide metabolism; black, coenzyme metabolism; cyan, lipid metabolism; light blue, cellular processes; brown, general function; gray, hypothetical and conserved hypothetical genes; pale green, structural RNAs). The third circle indicates the major IS element families as follows: black, ISne1 family; orange, ISne2; red, ISne3; green, ISne4; blue, ISne5; cyan, ISne6; magenta, ISne7; yellow, ISne8. The fourth circle indicates siderophore-receptor genes (blue) and pseudogenes (red). The fifth circle indicates *amo* (red), *hao* (green), the duplicated genes for EF-Tu (blue), the 7.5-kb tandem duplication (magenta) and the 339- and 318-bp repeats (black). RNA structural genes are indicated in the sixth circle. The inner two circles are the GC bias and GC skew.

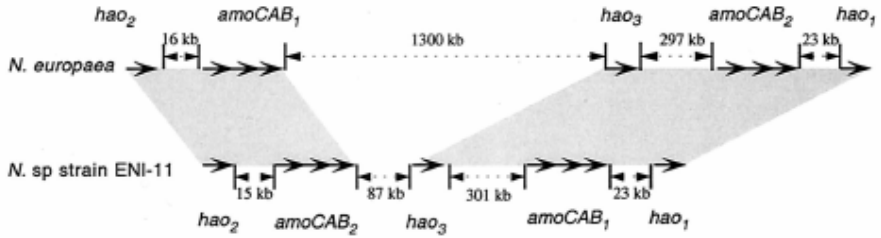


FIG. 2. Arrangement of *hao* and *amo* in *N. europaea* and *Nitrosomonas* sp. strain ENI-11. Arrows indicate the orientation of the genes. The nomenclature of the genes in *N. europaea* is with respect to their *Kpn*I fragment sizes for *hao* (38) and *Eco*RI fragment sizes for *amo* (37). The nomenclature for *Nitrosomonas* sp. strain ENI-11 follows that described by Hirota et al. (36). Distances between regions are indicated in kilobases and are not drawn to proportion. The gray areas indicate the regions similarly arranged.

TABLE 2. Complex repetitive sequences

Sequence group	Size (bp)	Copy no.	% Identity
Gene, operon, and/or region			
amoCAB, ORF4 and ORF5	4,833	2	>99
hao, ORF, c_{554} and c_{m552}	4,303	2	>99
hao, ORF, c_{554}	3,601	1	>99
tufB	1,193	2	>99
aat,' ORF, *pps4*, ORF, ORF, *glnS-hsU*'	7,510	2	100
IS elements			
ISne1 (single transposase, several strong database hits)	~1,250	27	>95
ISne2 (single transposase, strong hits to N and C terminus)	~1,012	16	>97
ISne3 (two transposases, similar to IS*401*)[a]	~1,316	13	>98
ISne4 (two transposases, several weak hits to both)	~843	10	>98
ISne5 (two transposases, similar to ISne4)	~815	9	>98
ISne6 (single transposase, several strong database hits)	~1,000	5	>98
ISne7 (single transposase, few weak database hits)	1,050	3	>99
ISne8 (single transposase, several strong database hits)	2,026	2	>99

[a] *Burkholderia cepacia*.

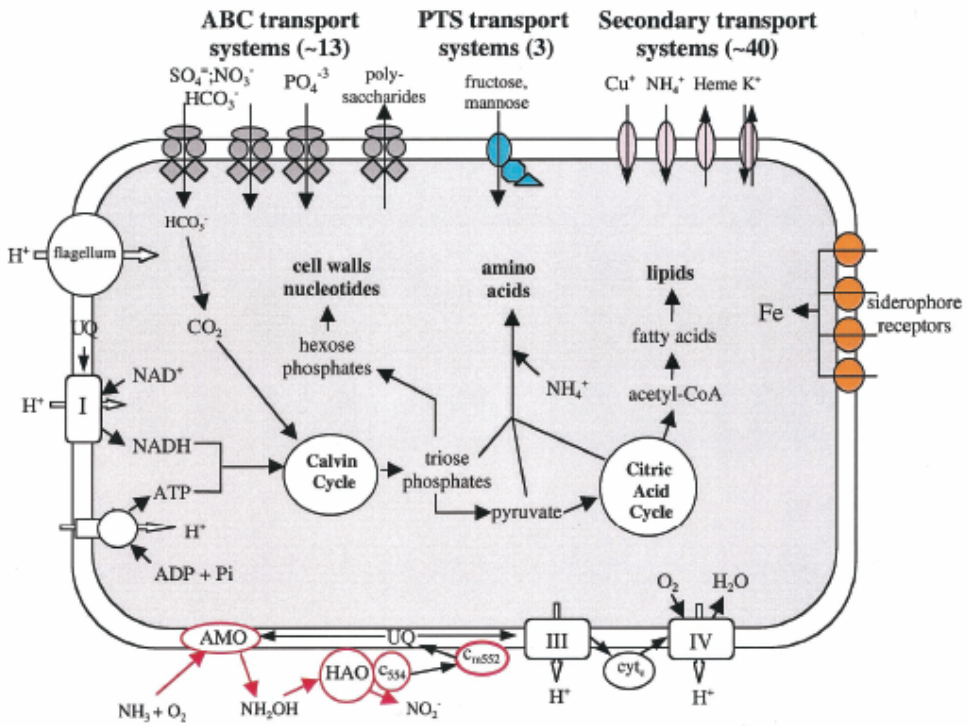
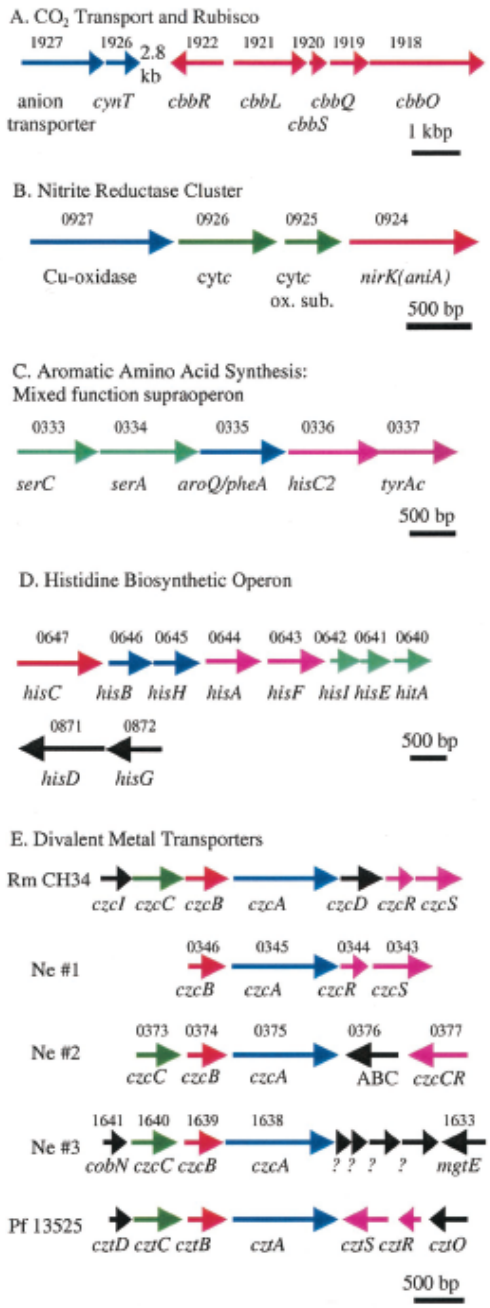


FIG. 3. Diagram of *N. europaea* cell. Processes primarily associated with the generation of a proton gradient are indicated on the bottom, and processes associated with utilization of the gradient are on the other sides. ATP and NADH production are indicated on the left. Transporters are indicated on the top and right. Not all transporters are indicated; the numbers in parentheses indicate the approximate numbers of each type. Major metabolic pathways and biosynthetic pathways are indicated in the center of the cell. The roman numbers refer to the enzyme complex I (NADH-ubiquinone reductase), complex III (ubiquinol-cytochrome *c* reductase), and complex IV (cytochrome *c* oxidase) in the respiratory chain.


A. CO_2 Transport and Rubisco
1927
1926
2.8 kb
1922
1921
1920
1919
1918
anion transporter
cynT
cbbR
cbbL
cbbQ
cbbS
cbbO
1 kbp
B. Nitrite Reductase Cluster
0927
0926
0925
0924
Cu-oxidase
cytc
cytc ox. sub.
nirK(aniA)
500 bp
C. Aromatic Amino Acid Synthesis: Mixed function supraoperon
0333
0334
0335
0336
0337
serC
serA
aroQ/pheA
hisC2
tyrAc
500 bp
D. Histidine Biosynthetic Operon
0647
0646
0645
0644
0643
0642
0641
0640
hisC
hisB
hisH
hisA
hisF
hisI
hisE
hitA
0871
0872
hisD
hisG
500 bp
E. Divalent Metal Transporters
Rm CH34
czcI
czcC
czcB
czcA
czcD
czcR
czcS
Ne #1
0346
0345
0344
0343
czcB
czcA
czcR
czcS
Ne #2
0373
0374
0375
0376
0377
czcC
czcB
czcA
ABC
czcCR
Ne #3
1641
1640
1639
1638
1633
cobN
czcC
czcB
czcA
? ? ? ?
mgtE
Pf 13525
cztD
cztC
cztB
cztA
cztS
cztR
cztO
500 bp

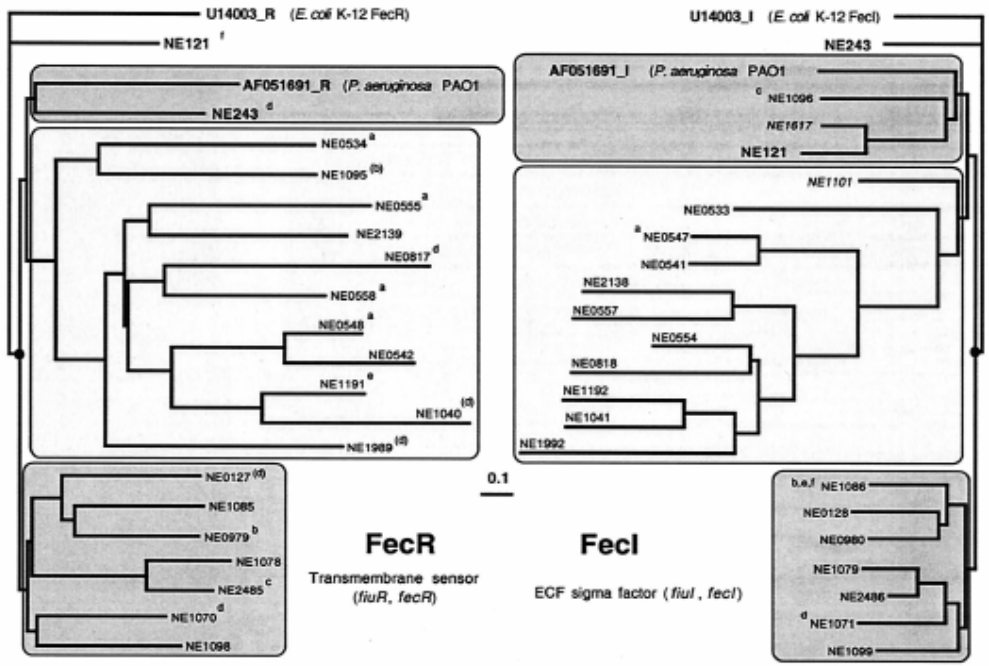


FIG. 5. Phylogeny of FecI and FecR homologous proteins and associated iron siderophore receptors. Distance-neighbor-joining trees were derived from CLUSTALW alignments of FecI- and FecR-homologous protein sequences that were deduced from identified ORFs in the genome of *N. europaea*. Sequences of identified functional FecI (FiuI) and FecR (FiuR) proteins from *E. coli* K-12 (U14003) and *P. aeruginosa* PAO1 (AF051691) were obtained from GenBank and used as a reference for the alignments. Designations of *N. europaea* proteins with high similarity to the FecIR proteins from *E. coli* and *P. aeruginosa* are given in boldface. Designations of FecI proteins without a respective FecR are given in italics. Putative iron siderophore sensing receptors that preceded or succeed a *fecIR* gene tandem in the genome are indicated with superscript letters as follows: a, ferrichrome-iron receptor 3 PCC6803 (D90899); b, ferrichrome-iron receptor *B. bronchioseptica* (U77671); c, hydroxamate ferrisiderophore receptor PAO1 (AF051691); d, unidentified ferric siderophore receptor PAO1 (U33150); e, ferripyoverdine receptor PAO1 (L10210); and f, TonB-dependent outer membrane receptor PAO1 (AE004674). Letters in parentheses indicate that the ORF is probably truncated. An additional gene encoding a ferrienterobactin receptor similar to AF083948 was found not associated with FecIR (data not indicated).

Purple bacteria

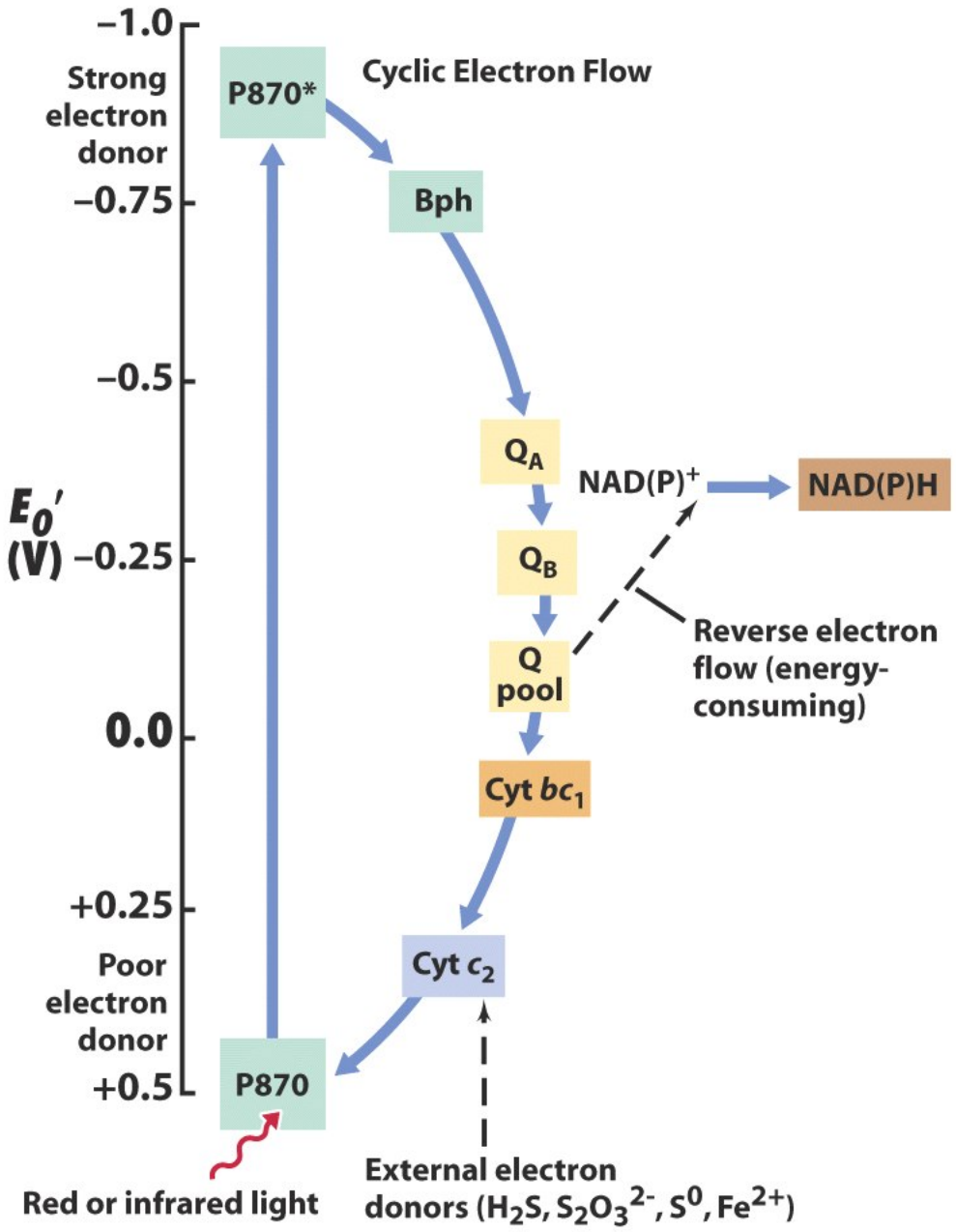
Cyclic

NAD(P) reduction requires -0.32 V

NAD(P)H for CO_2 fixation generated by reverse e^- flow (requires energy to push e^-s against potential): further metabolic burden on already energy - poor process

ATP generated by PMF built during electron transport

Anoxygenic photosynthesis



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