INTIMATE STRANGERS:
MICROBIAL PARTNERS IN THE NATURAL WORLD

OLLI

SPRING 2020

LECTURE 3:
MICROBES AS COMMUNITY BUILDERS

MICROBIAL COLONIZATION OF DRY LAND

WHENCE MICROBIAL DIVERSITY

THE MICROBIAL ENVIRONMENT

MICROBIAL METABOLIC DIVERSITY

MICROBES AND NUTRIENT CYCLES

DISTURBANCES IN NUTRIENT CYCLES

THE LAST FRONTIER: COLONIZATION OF LAND

- WHAT IS A TERRESTRIAL ENVIRONMENT?
  - NON-AQUATIC? HOWEVER, EVEN FULLY AQUATIC ECOSYSTEMS, SUCH AS LAKES AND COASTAL ENVIRONMENTS, COVER A WIDE SPECTRUM OF MIXED ENVIRONMENTS WHERE AQUATIC AND NON-AQUATIC LANDSCAPES DEVELOP AND OVERLAP
  - GROWING EVIDENCE INDICATES THAT NON-AQUATIC ENVIRONMENTS WERE COLONIZED BY MICROBES EARLY IN EARTH'S HISTORY, CONSISTENT WITH THE EXTENT OF MODERN MICROBIAL LIFE ON ANALOG "BARREN" LANDS (REMEMBER ATACAMA…)
- POTENTIAL COLONIZERS:
  - IN COASTAL ENVIRONMENTS MICROBES WERE LIKELY TO HAVE BEEN PERIODICALLY EXPOSED AND DESICCATED, AND LIKELY DEVELOPED ADAPTATIONS FOR LONG-TERM DESICCATION, SALINITY FLUCTUATIONS AND HIGH UV RADIATION

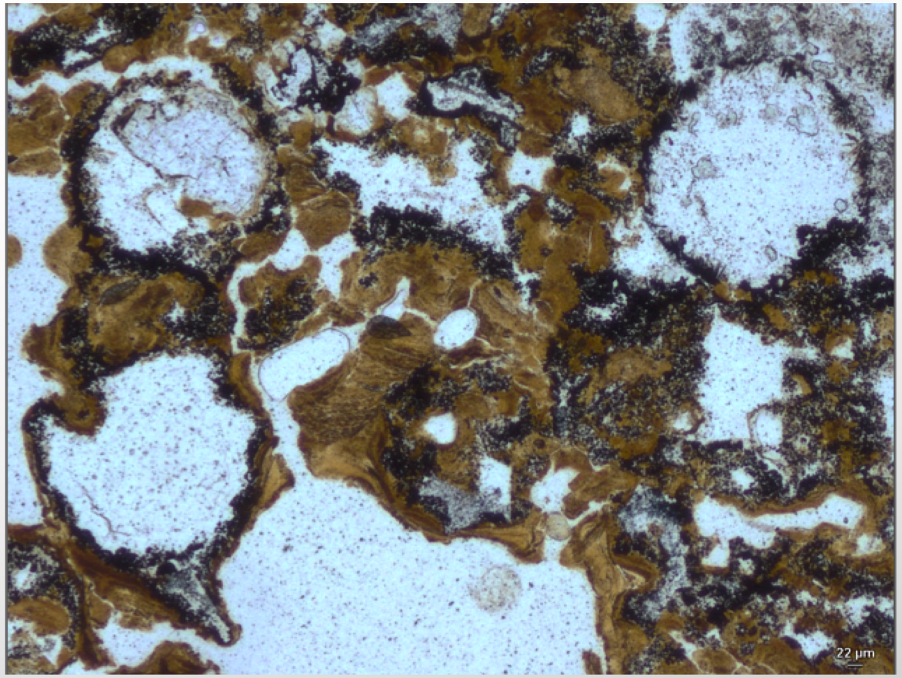
- IN MAY 2017, EVIDENCE OF THE EARLIEST TERRESTRIAL LIFE FORM WAS FOUND IN 3.48-BILLION-YEAR-OLD GEYSERITE AND OTHER RELATED MINERAL DEPOSITS (OFTEN FOUND AROUND HOT SPRINGS AND GEYSERS) UNCOVERED IN THE PILBARA CRATON OF WESTERN AUSTRALIA

Dresser formation – Pilbara Craton, Western Australia

DRESSER FORMATION – PILBARA CRATON, WESTERN AUSTRALIA

- CRATON: AN OLD AND STABLE PART OF THE CONTINENTAL LITHOSPHERE (CRUST AND UPPERMOST MANTLE), COMPOSED OF ANCIENT CRYSTALLINE BASEMENT ROCK, WHICH MAY BE COVERED BY YOUNGER SEDIMENTARY ROCK
- SANDSTONES AT STRELLEY: FOSSILS OF SULFUR-PROCESSING BACTERIA. THE MINERALIZED SPHERES, WHICH WERE FOUND ON AN ANCIENT BEACH AND APPEAR CELL-LIKE , WERE CHEMICALLY ANALYZED, REVEALING THAT THEY USED SULFUR FOR FUEL

Silicified gas bubbles
Djokic et al, *Nature communications* 8, May 2017



MICROBIAL LIFE ON THE SURFACE

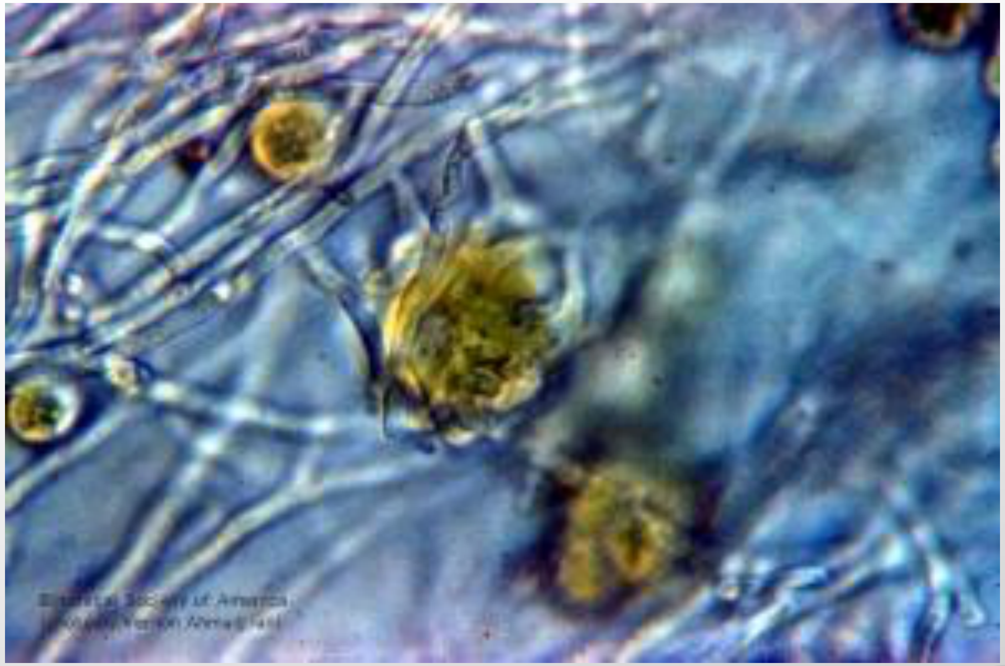
- RAPID AND GLOBAL DEVELOPMENT OF LIFE ON EARTH, WITH LIFE FORMS ADAPTED TO LIVE ON LAND CA. 2.5 GA; 2,000 MA BEFORE THE EARLIEST FOSSIL RECORD OF LAND PLANTS
- OXYGENIC PHOTOSYNTHESIS WAS A PARTICULARLY IMPORTANT CAPABILITY OF TERRESTRIAL ORGANISMS, BECAUSE THEIR ENERGY SOURCE (LIGHT), REDUCTANT POWER (WATER), AND CARBON SOURCE (CO_2) ARE READILY AVAILABLE → CYANOBACTERIA
- CYANOBACTERIA CAN ALSO FIX N_2
- THEY TEND TO FORM MICROBIAL MATS
- THEY BECOME NICHES FOR OTHER MICROBES TO COLONIZE: HETEROTROPHS FEEDING ON EXUDATES OF CYANOBACTERIA, MICROBES THAT SECRETE MUCOPOLYSACCHARIDES, PROVIDING GLUE FOR THE MICROBIAL MATS

SOIL

- EVENTUALLY FUNGI ARRIVE
- LICHENS WHICH ARE SYMBIOTIC COMBINATIONS OF A FUNGUS AND ONE OR MORE PHOTOSYNTHESIZERS (GREEN ALGAE OR CYANOBACTERIA), ARE IMPORTANT COLONIZERS OF DRY ENVIRONMENTS
- THEIR ABILITY TO BREAK DOWN ROCKS CONTRIBUTES TO SOIL FORMATION
- TERRESTRIAL MICROBES CAN DRIVE CHEMICAL TRANSFORMATIONS IN SOILS: AFFECT THE REACTIVITY OF MINERAL SURFACES WITH SECRETED METABOLITES, CHANGING THE PH AND REDOX POTENTIAL OF THE MICROENVIRONMENT, SECRETING METAL LIGANDS AND OTHER ORGANIC COMPLEXES THAT REACT WITH SOLUTES AND MINERALS

LICHENS: A SUCCESSFUL MICROBIAL MUTUALISM STORY

- COMPOSITE ORGANISM: CYANOBACTERIA OR ALGAE (EUKARYOTIC PHOTOSYNTHETIC PROTISTS) LIVING AMONG FILAMENTS OF FUNGI
- CA. 6% OF EARTH'S SURFACE COVERED BY LICHENS
- CA. 20,000 KNOWN SPECIES
- THEY ARE PIONEER SPECIES IN LAND COLONIZATION
- TOLERANT OF PERIODS OF DESICCATION



MICROBIAL LIFE UNDERGROUND

- GEOTHERMAL VEINS, AQUIFERS, SOIL SUBSURFACE, ALL TYPES OF CAVES
- UNDERGROUND MICROBES REQUIRE A CHEMOSYNTHETIC METABOLISM FOR PRIMARY PRODUCTIVITY, RELYING ON THE OXIDATION OF SULFUR AND IRON COMPOUNDS TO SUPPORT GROWTH
- THESE METABOLIC PATHWAYS ARE LESS ENERGETIC THAN PHOTOSYNTHESIS → LIFE WOULD HAVE BEEN SLOW-GROWING, LESS DYNAMIC IN TERMS OF DIVERSITY AND INTERACTIONS, AND MORE GEOGRAPHICALLY CONTAINED
- MAY HAVE IMPACTED THE SUBSURFACE (CAVE FORMATION, BURIED OIL AND DISSOLVED ORGANIC MATTER CONSUMPTION, METHANE PRODUCTION, ETC.)

IMPACT OF TERRESTRIAL MICROBIAL LIFE

- CONTINUOUS OXYGENATION OF THE ATMOSPHERE (WITH CONSEQUENCES FOR THE STRATIFICATION OF THE OCEANS, THE FORMATION AND MAINTENANCE OF THE OZONE LAYER, AND THE PRECIPITATION OF OXIDES, AMONG OTHERS)
- GASEOUS BYPRODUCTS, SUCH AS OXYGEN PRODUCED ON THE LAND WOULD BE RELEASED DIRECTLY INTO THE ATMOSPHERE AND NOT DISSOLVED IN THE OCEANS FIRST
- LAND-BASED LIFE COULD HAVE BEEN PIVOTAL FOR THE EARLY OXYGENATION OF THE ATMOSPHERE
- COASTAL AND INLAND SETTINGS WERE TRANSFORMED BY THEIR MICROBIAL COLONIZERS INTO ORGANIC- AND NUTRIENT-RICH SUBSTRATES THAT COULD LATER BE EXPLOITED BY MORE EVOLVED COMMUNITIES AND ORGANISMS

SO, CA. 2 BILLION YEARS AGO…

- MICROBIAL LIFE HAS NOT ONLY ARISEN, BUT COLONIZED ALL KINDS OF ENVIRONMENTS
- VERY EARLY METABOLIC DIVERSIFICATION OF MICROBES (DIFFERENT ENERGY SOURCES, DIFFERENT CARBON SOURCES)
- ADAPTATIONS TO DIFFERENT ENVIRONMENTS

- WHAT CAUSES THIS DIVERSIFICATION?
- ARE THE SAME PROCESSES EXTANT TODAY?

GENETIC VARIATION – WHAT IT IS AND HOW IT HAPPENS

- CHANGES IN HERITABLE TRAITS

- MUTATIONS
- RESHUFFLING OF GENES
- MIGRATION BETWEEN POPULATIONS (GENE FLOW)

GENETIC DIVERSITY – MUTATIONS

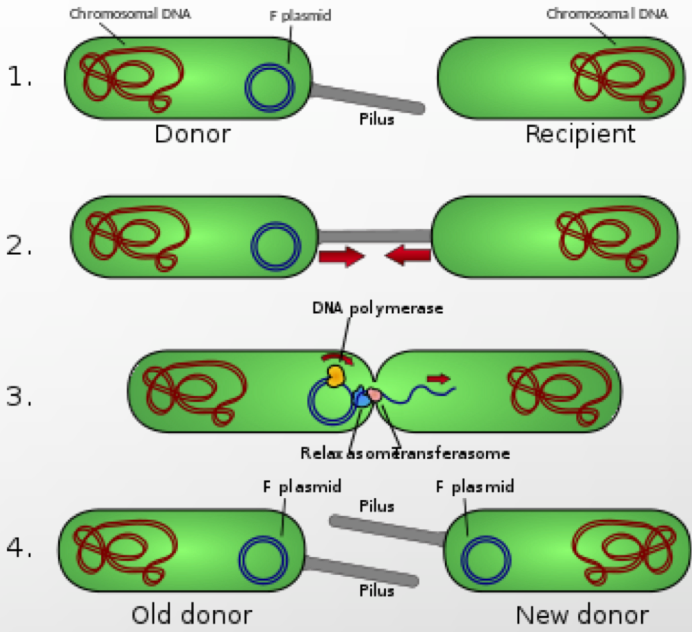
- SPONTANEOUS: ERRORS DURING DNA REPLICATION
  - RATE: 10^{-6} – 10^{-7} PER 1,000 BASES PER REPLICATION CYCLE
- ERRORS DURING DNA REPAIR
- INSERTION OR DELETION OF GENETIC MATERIAL
- INDUCED: MUTAGENS

GENETIC DIVERSITY – RECOMBINATION AND GENE FLOW

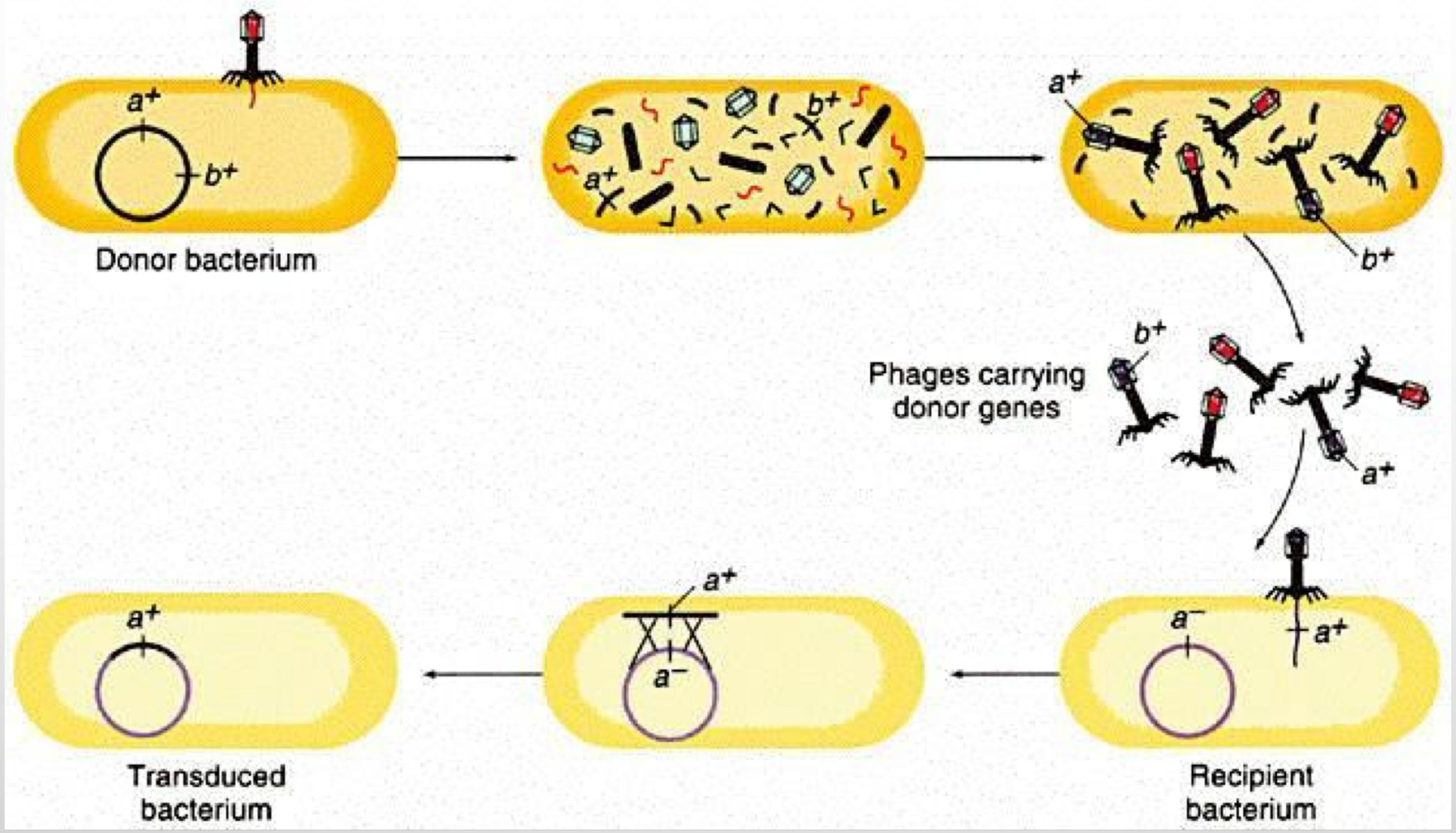
- EXCHANGE OF GENES BETWEEN ORGANISMS, POPULATIONS AND BETWEEN SPECIES
- HORIZONTAL GENE TRANSFER:
- BETWEEN MICROBIAL PARTNERS
- VIRUS-MEDIATED
- DIRECT UPTAKE OF DNA FROM THE ENVIRONMENT
- MOBILE GENETIC ELEMENTS

BETWEEN MICROBIAL PARTNERS – CONJUGATION

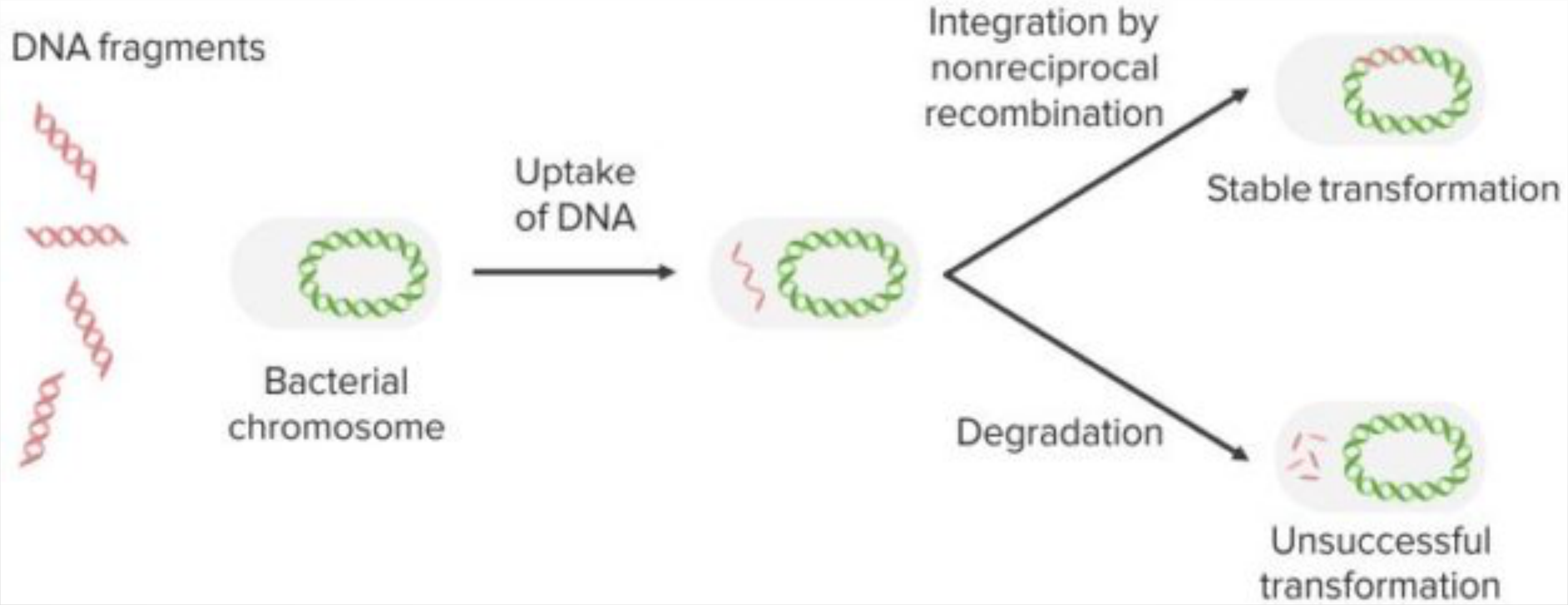
- DONOR CELL, CARRYING A MOBILE GENETIC ELEMENT, PRODUCES A PILUS (HAIR-LIKE EXTENSION)
- PILUS ATTACHES TO RECIPIENT CELL AND BRINGS THE TWO CELLS TOGETHER
- THE DONOR INJECTS THE DNA INTO THE RECIPIENT
- TOGETHER WITH THE MOBILE GENETIC ELEMENT, SOMETIMES PORTIONS OF THE DONOR'S DNA ARE ALSO TRANSFERRED → THEY CAN RECOMBINE WITH THE RECIPIENT'S DNA



VIRUS-MEDIATED – TRANSDUCTION

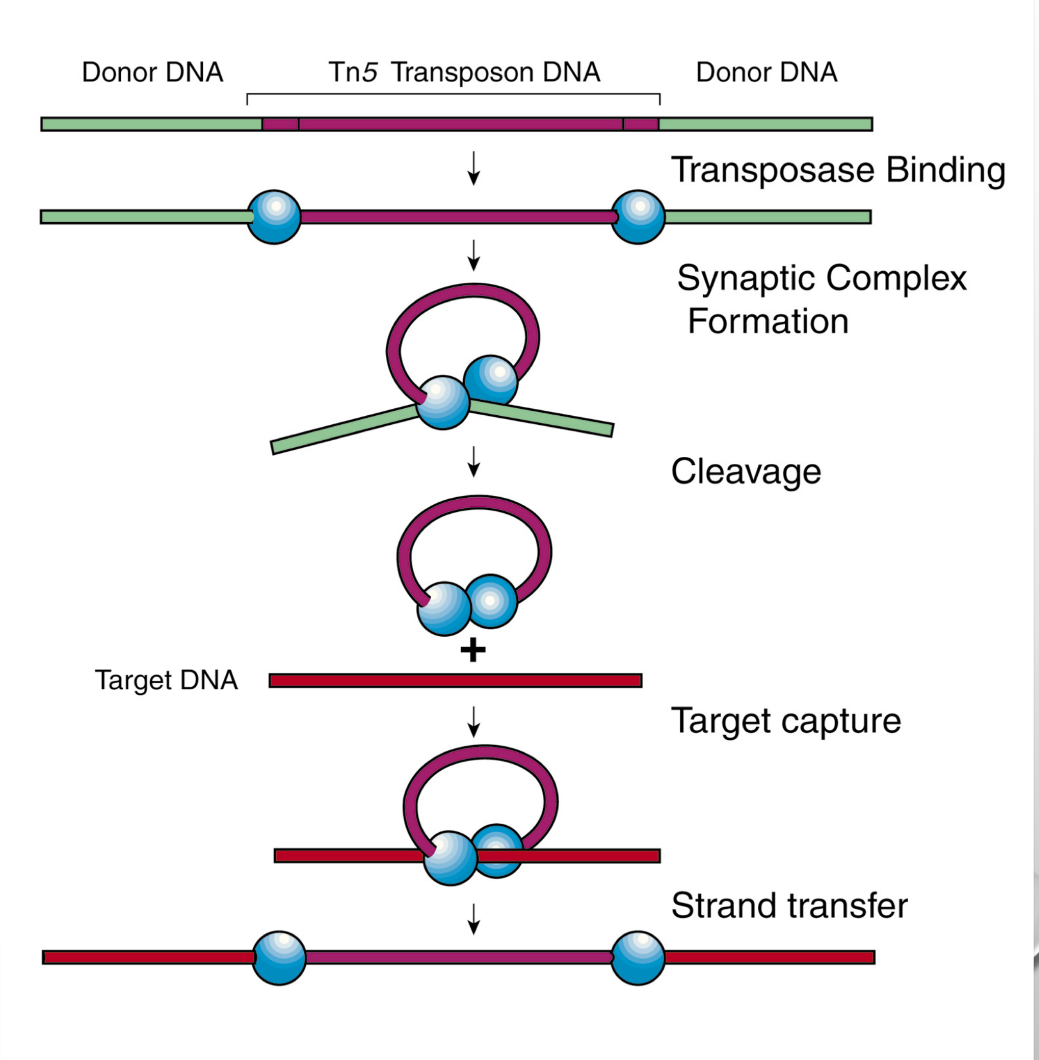


DIRECT DNA UPTAKE – TRANSFORMATION



MOBILE GENETIC ELEMENTS

- GENETIC MATERIAL THAT CAN MOVE AROUND WITHIN A GENOME, OR THAT CAN BE TRANSFERRED FROM ONE SPECIES TO ANOTHER
- THEY CAN CARRY ANTIBIOTIC-RESISTANCE AND VIRULENCE GENES
- COMMON AMONG BACTERIA, EVEN AMONG VERY DISTANTLY RELATED ONE
- THEY CARRY ALL THE NECESSARY GENES TO JUMP
- INSERTION INTO THE TARGET DNA MOLECULE CAN BE RANDOM (NO SITE-SPECIFICITY)

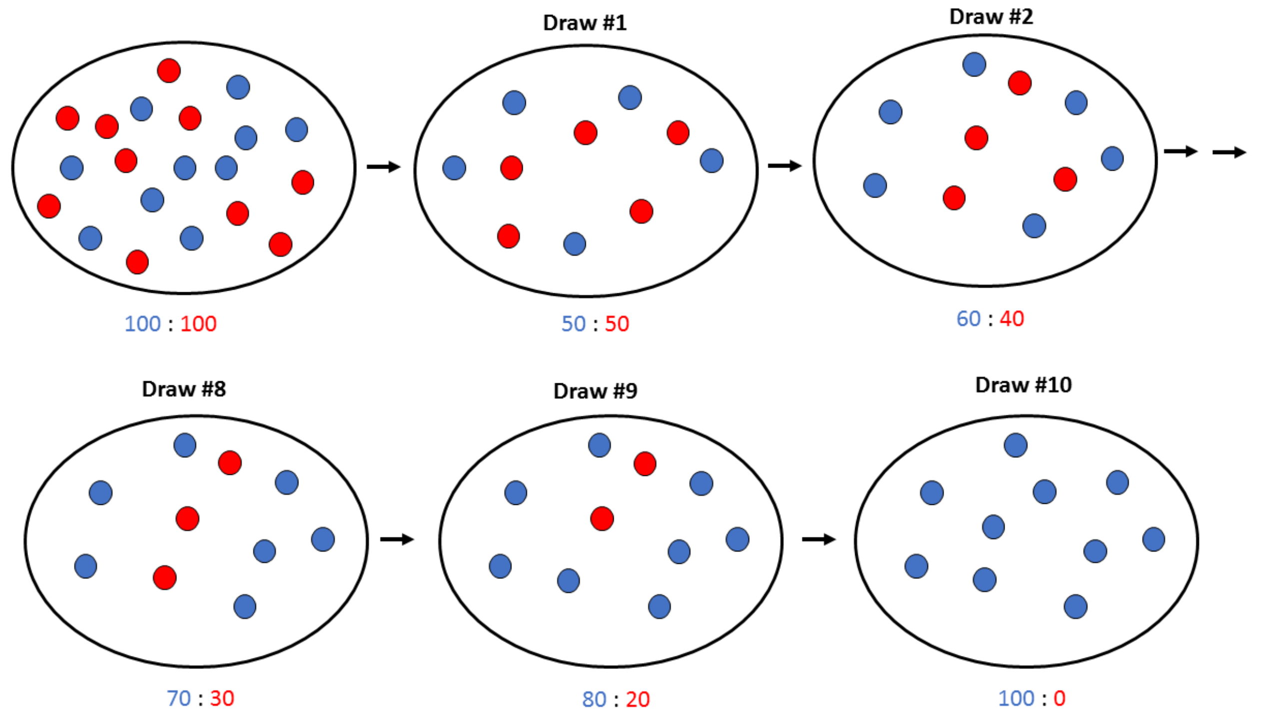


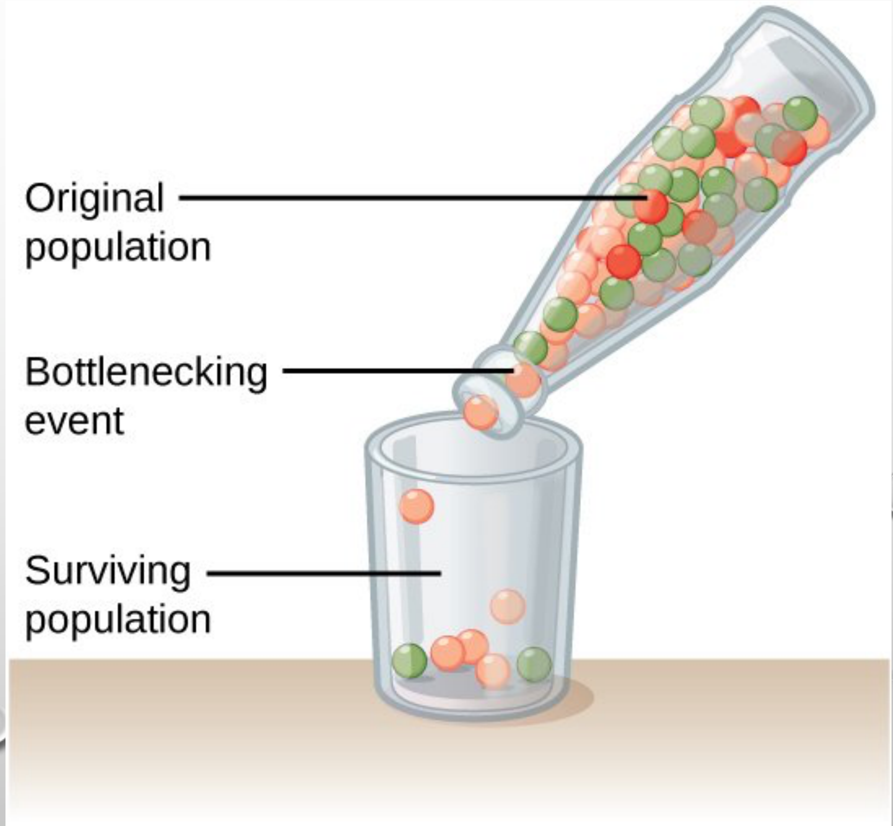
HOW DOES THE MICROBIAL **POPULATION** CHANGE?

- SELECTION: GOOD OLD DARWINIAN SURVIVAL OF THE FITTEST
- GENETIC HITCHHIKING: GENES CLOSE TOGETHER MAY NOT ALWAYS BE SHUFFLED AWAY FROM EACH OTHER → GENES THAT ARE CLOSE TOGETHER TEND TO BE INHERITED TOGETHER
- RANDOMLY, THROUGH **GENETIC DRIFT:**
- RANDOM FLUCTUATIONS OF GENETIC VARIANTS WITHIN A POPULATION FROM ONE GENERATION TO THE NEXT
- WHEN SELECTIVE FORCES ARE ABSENT OR RELATIVELY WEAK, ALLELE FREQUENCIES ARE EQUALLY LIKELY TO ***DRIFT*** UPWARD OR DOWNWARD AT EACH SUCCESSIVE GENERATION (PROBABILITY WILL DO THIS; NO MYSTERIES INVOLVED)
- THIS DRIFT CAN RESULT IN A VARIANT DISAPPEARING FROM THE POPULATION, OR BECOMING FIXED
- THIS IS JUST CHANCE! (AND LOTS OF TIME, COUNTED AS GENERATIONS)

GENETIC DRIFT

- EVEN IN THE ABSENCE OF SELECTIVE FORCES, GENETIC DRIFT CAN CAUSE TWO SEPARATE POPULATIONS THAT BEGAN WITH THE SAME GENETIC STRUCTURE TO DRIFT APART INTO TWO DIVERGENT POPULATIONS WITH DIFFERENT SETS OF ALLELES
- THIS CAN HAVE DRAMATIC EFFECTS DURING EVOLUTIONARY “BOTTLENECKS”





THE MICROBIAL ENVIRONMENT

- HABITAT IS GOVERNED BY PHYSICAL AND CHEMICAL CONDITIONS AND HOW THOSE CONDITIONS INFLUENCE THE METABOLIC CAPABILITIES OF THE MICROBIAL RESIDENTS
- SINCE MICROBES ARE SMALL, THEY EXPERIENCE A SMALL LOCAL ENVIRONMENT
- ERGO, NUMEROUS MICROENVIRONMENTS HARBORING DIFFERENT MICROBIAL SPECIES CAN COEXIST WITHIN A GIVEN HABITAT
- DIFFUSION OFTEN DETERMINES THE AVAILABILITY OF RESOURCES → THERE CAN BE STRATIFICATION
- RESOURCES TYPICALLY ENTER AN ECOSYSTEM INTERMITTENTLY (THINK "FEAST-OR-FAMINE") → MICROBES GROW IN "SPURTS"
- COMPETITION FOR RESOURCES MAY BE INTENSE
- MICROBES CAN ALSO COOPERATE (SYNTROPHY)

COMPETITION AND COOPERATION

- COMPETITION FOR RESOURCES MAY BE INTENSE
- INDIVIDUALS IN A POPULATION MAY BE IN COMPETITION WHEN NUTRIENTS ARE LIMITING. IF THE ECOLOGICAL OPPORTUNITY ARISES, INTRASPECIES COMPETITION CAN LEAD TO SELECTION FOR THE DIVERSIFICATION OF A BACTERIAL POPULATION
- SOME COMPETITIVE STRATEGIES: ACCUMULATING AND STORING SPECIFIC NUTRIENTS; BLOCKING ACCESS TO FAVORABLE HABITATS (SUCH AS BINDING SITES ON A SURFACE); PRODUCING ANTIMICROBIAL TOXINS; AND INTERFERING WITH COMPETITORS' SIGNALING

- MICROBES COULD DECIDE TO COOPERATE → SYNTROPHY
- ONE SPECIES LIVES OFF THE PRODUCTS OF ANOTHER SPECIES
- IMPORTANT IN NUTRIENT CYCLES AND MICROBIAL FOOD WEBS
- IMPORTANT IN BREAKDOWN OF ORGANIC ENVIRONMENTAL POLLUTANTS

MICROBIAL HOMES – THE MAT

- SURFACES, NO MATTER WHAT KIND. ANY NATURAL OR ARTIFICIAL SURFACE **WILL** BE COLONIZED BY MICROBES
- MICROBES TEND TO CLUMP TOGETHER INTO "COLONIES"
- IF CONDITIONS ARE RIGHT, WITH FEW OR NO PREDATORS, THEY CAN FORM THICK MICROBIAL MATS: HIGHLY COMPLEX AND VERY STABLE ASSEMBLAGES OF DIVERSE MICROBES

Cross section of microbial mats showing layers of pigmented bacteria

A MICROBIAL MAT GALLERY – YELLOWSTONE

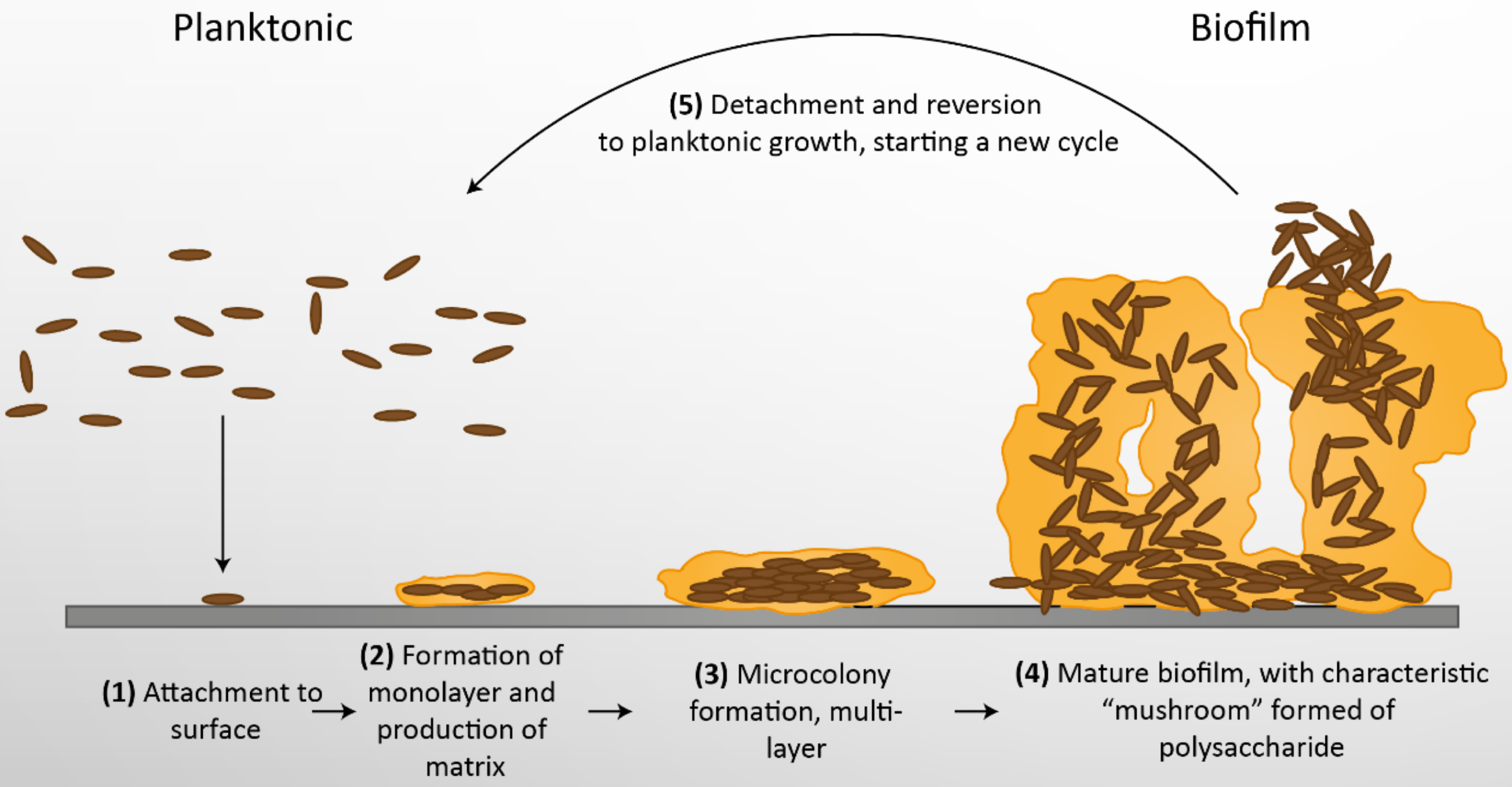
MICROBIAL HOMES – BIOFILMS

- ASSEMBLAGE OF MICROBIAL CELLS, ATTACHED TO A SURFACE
- ENCLOSED IN AN ADHESIVE MATRIX, THE PRODUCT OF EXCRETION AND ALSO DEAD CELLS
- BIOFILMS TYPICALLY CONTAIN MANY TYPES OF MICROBES
- BIOFILM COMMUNITIES ARE ALWAYS MORE DIVERSE THAN THE WATERS AROUND THEM
- BIOFILMS ARE INHERENTLY TOLERANT TO ANTIBIOTICS (A MICROBE IN A BIOFILM MAY BE 1000 TIMES MORE TOLERANT TO AN ANTIMICROBIAL AGENT THAN FREE-SWIMMING CELLS OF THE SAME SPECIES
- REASONS: REDUCED PENETRATION OF THE ANTIBIOTIC, SLOWER GROWTH (SOME ANTIBIOTICS WORK ON DIVIDING CELLS), HIGHER LEVELS OF EXPRESSION OF GENES THAT INCREASE TOLERANCE TO STRESSORS
- THINK: DIFFICULT-TO-TREAT INFECTIONS, “FOULING” IN INDUSTRIAL SYSTEMS WHERE SURFACE GROWTH CAN IMPAIR PROCESSES

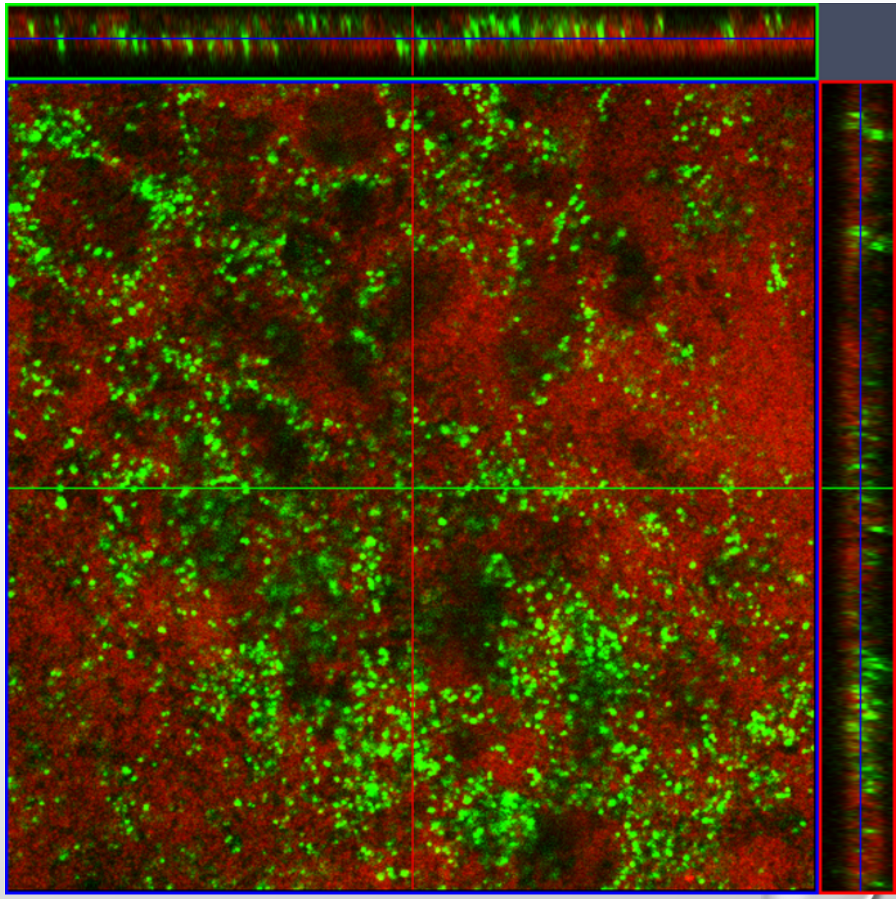
BIOFILMS ARE GOOD IF YOU ARE A MICROBE

- INCREASED SURVIVAL: RESIST PHYSICAL FORCES, AVOID BEING EATEN, RETARD PENETRATION OF TOXIC MOLECULES
- ALLOW CELLS TO REMAIN IN A FAVORABLE ENVIRONMENT
- LIVE IN CLOSE ASSOCIATION → FACILITATE CELL-TO-CELL COMMUNICATION, MORE OPPORTUNITIES FOR NUTRIENT AND GENETIC EXCHANGE
- MAY HAVE BEEN THE “ANCESTRAL” MODE OF GROWTH. GOING AT IT SOLO MAY BE FOR MICROBES ADAPTED TO LIFE AT EXTREMELY LOW NUTRIENT CONCENTRATION

MICROBIAL BIOFILMS



Biofilm formation



Pseudomonas (red) and *Staphylococcus* (green)