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All righty. So we've been talking about, the last time we talked about the different ways that this extraordinary process called evolution has resulted in different ways that organisms exploit the carbon and energy sources that are available on earth. And as we talked about that we find that whatever is thermodynamically possible in terms of redox gradients in the environment you will find an organism that has evolved to exploit it.

And one thing I haven't mentioned to you guys yet -- Maybe I've mentioned it but I haven't driven it home is that in the microbial world right now 99.9% of the microbes that live on earth have never been cultivated. So it's a vastly unknown universe, the details. So the metabolic pathways that I'm describing here are just the tip of the iceberg in terms of what's possible.

So last time we were talking at the biochemical scale. This time we're now going to scale up and think of these biochemical processes on a global level. And we're going to talk about primary productivity which is really just another word for the collective photosynthesis of all of the photosynthesizers on earth. So who are the dominant primary producers? Well, we've already talked about this. And just to get ourselves oriented let's think of in water the primary photosynthetic organisms, the primary producers are phytoplankton.

And let's just look at one phytoplankton cell, OK? This is a single cell so this would be maybe ten microns in size. And inside that cell we have a chloroplast, and you've learned all this in other lectures and including my lectures, which takes up CO₂ and evolves oxygen and makes sugars which go to, what's the organelle where respiration takes place? Mitochondria.

Which goes to the mitochondrion and is respired. CO₂ is evolved and oxygen is taken up. So this little single cell gets through life through photosynthesis primarily, but it also takes the products of photosynthesis and burns them inside the cell. So this is what we call respiration. And it's important to remember that even photosynthetic organisms respire, OK? But then there's this whole other group of organisms that last time we called heterotrophs that can only respire.

They rely on the photosynthetic product from photosynthetic organisms. So that's in water. And then on land the main primary producers, productivity are plants. And we'll just symbolize these as a tree. And we all know that the tree takes up CO₂, evolves oxygen. If you blow this up, you just take a leaf, OK? That's a blowup. And then you blowup again and take a cell from the leaf.

This cell is identical in function to the single microscopic phytoplankton cell, OK? So the process in both of these ecosystems, this could be grass, it could be moss, it could be anything else, the process is the same in terms of what's involved in productivity. OK. Now, you have a handout for this lecture that has a lot of the definitions that I'm going to now very briefly put on the board.

Oh, I should tell you also that in the last ten minutes of the lecture I'm going to show you another incredible clip from the Blue Planet series that I showed you last time so you have something to look forward to. So let's define some terms. Biomass we're going to call B. And as I said this is all in the handout. So I'm just going to give you the short version here. And the units of this can be of course anything, but normally it's something like grams carbon per meter squared.

And what does that mean? Well, it means if you have, in a terrestrial ecosystem, OK, where you have trees, it would mean that you would calculate the biomass. You'd take a square meter and you'd integrate up and collect all of the biomass in that surface area, OK? So that's what that means. So grams carbon in that square meter. For an aquatic ecosystem it's the opposite.

You take a square meter of the surface water, let's put some waves on here, and you integrate all the way down. How far? When will you not have anymore primary, oh, no, biomass? When will you no longer have any more photosynthetic biomass in the oceans or in a lake? Pycnocline. Oh, that's a good answer. Not necessarily, though. But it often corresponds to that. The pycnocline is a density gradient in aquatic ecosystems.

But what is absolutely essential for photosynthesis? Light. Light. So you go down until there's no light. Absolutely. There won't be any photosynthesis where there's no light. This is the one thing we know for sure, OK? And that's usually in the oceans around 200 meters. And in lakes it depends on how rich they are. In the Charles River it's about one meter because it's such a mess.

In fact, well, I shouldn't say a mess, but it's very productive. In fact, legend has it, and I don't know if this is true, that it's actually safe to swim in the Charles in terms of the water quality, but the reason you're not supposed to swim is because the visibility is so bad that if anything happened they'd never find you. But I don't know if that is true.

That could be an urban legend. OK, so we're going to define gross primary productivity. GPP, gross primary productivity is the rate of photosynthesis -- -- and grams carbon per meter squared per year. And of course the units here are not, the absolute units, this could be per day and this could be per square millimeter if you wanted, but the units are amount per unit area per unit time, OK? And then we're going to define the respiration rate, the respiration of the autotrophs.

So this would be the respiration rate of the photosynthetic organisms, which is why we call them $R_{sub A}$. And that's going to have the same units, OK? So it's grams carbon per meter squared per year respired. And net primary productivity is then gross primary productivity minus $R_{sub A}$ so net primary productivity of an ecosystem is the amount of carbon CO_2 that's drawn into the system through photosynthesis minus the amount that was respired by the plants, by the organisms that did the photosynthesis.

In a sense, you can think of it as the amount of carbon that actually goes into a plant growing, OK, that goes into the biomass of a tree or that goes into the division of a single celled phytoplankton into two phytoplankton. And then a lot of that is lost through respiration. OK. We can also define mean residence time -- -- as MRT, which is the biomass divided by the net primary productivity.

So what are the units of the mean residence time? It should be obvious but -- Years, right, or time. Mean residence time is time. And that's really, if you want to think about it, if you think of yourself as a carbon atom that's drawn into a tree through photosynthesis, it's the average amount of time you will spend, your one atom in that tree. OK? It's the average residence, the mean residence time.

Well, actually, that's wrong, right? It's not the amount of time that you, that one atom will spend, but it's on average the amount of time that atoms will spend in the tree. OK. And then the fractional turnover -- -- is equal to one over the mean residence time. And it has the units of obviously years to the minus one. And it's the fraction, if you think of a tree again, it's the fraction of the carbon in that tree that is renewed by new carbon every year.

Now, these two concepts will become very important again when we start to talk about global biogeochemical cycles. And we'll talk about the residence time, the various elements in various components in the earth system. OK. So now let's go on and look at, first of all, I should have shown this slide last time. I'm trying to not walk around too much because this fellow is filming me or filming these classes.

But we should briefly take a look at the absorption spectrum of all of the plants in the biosphere. Could we turn the lights down a little? Or I guess I'm in charge of that. There. A little bit better maybe. This is the absorption spectrum of the pigment chlorophyll, chlorophyll A that is the pigment that all green plants have and they use to absorb sunlight. And you'll notice that over the course of evolution all of these white bands are accessory pigments.

That different organisms have evolved to also capture light. And they pass on that energy to the chlorophyll molecule. And the point is that if you look across all of the visible light and even beyond there are pigments that have evolved to capture that solar energy collectively in the ecosystem. OK, so let's look at, now we're going to look at world net primary productivity. So essentially photosynthesis on a global scale.

And I'm going to tell you right up front. These numbers are extremely approximated. And I've taken these numbers from various textbooks. Your textbook doesn't even have a table like this in it. In fact, your textbook is very weak in this section of biology. But there are always tradeoffs in choosing textbooks. So I've taken this from textbooks and I've rounded off these numbers. And so I just want you to go through and understand the structure of the table.

The idea is not to memorize particular numbers but understand and have a feeling for the relative amounts of productivity in different ecosystems. So, first of all, here's our units of grams per year, world net primary productivity. These are grams of carbon, OK? And if we first look at the total amount on land, in this particular table is 177 versus the marine total is 54.

But the new estimates, I've taken this out of sort of more primarily literature than textbooks, really show these numbers to be more like this. That shows you how variable this is. It changes every decade. Showing that the amount of photosynthesis in the oceans is roughly on par with the amount on land. And to remind you of our units here, weight-wise this is 50 to 70 billion Volkswagen's worth of carbon.

I mean that's a lot of carbon every year that is going into these ecosystems. OK, so let's look and dissect the table a little bit. Looking at tropical forests like the rainforest in the Amazon that are some of the most productive ecosystems in the world. You can see that over here their net primary productivity per meter squared is 2,000. And then you look down here at the open ocean which on a per meter squared basis, a very unproductive ecosystem, there are tiny little phytoplankton, is 100.

But looking further, before I get to the but which is the punch line. That's the trouble with animation. The biomass in the tropical forest is enormous, obviously trees, whereas the biomass in the open ocean is very tiny. But if we look at the percent of the surface of the earth that is covered by these two different ecosystems the open ocean is huge compared to the tropical forest.

So on a global scale, because of the aerial coverage here these two ecosystems contribute equally, OK? So it's a combination of net primary productivity and the coverage of the global ocean. OK. Let's go back to that for a minute. So let's -- -- talk about turnover times or mean residence times. Just eyeballing it, can you give me an estimate in terms of days, months, years, decades, centuries, order of magnitude for the mean residence time of carbon in all the phytoplankton in a marine ecosystem? Is it days, months, years, centuries, decades? Well, don't guess.

Well, you can guess but minutes is wrong. So having guessed minutes is wrong now you use your analytical brain and you look at this, mean residence time, which is biomass divided by net primary productivity. Here's the biomass. Round that off. And here's the net primary productivity. And the units here is years. Like a month did I hear? I didn't hear. Right. It's about one-tenth of year which is about a month. About a month.

Does everybody follow that? It's just to round this off, five over 50 is 0.1, biomass over NPP. How about for the terrestrial ecosystem, what's the average amount of time a carbon atom spends in the average tree? Years, right? Decades. Many years. Maybe decades to centuries. This is a way we think about these things. We don't have an exact number. But you want to get an order of magnitude feeling.

So carbon is turning over very, very fast in the marine ecosystem but very slowly in the terrestrial ecosystem. And the simple way to think about that is that phytoplankton don't have trunks, but there's a more complicated way to think about it. OK, so now, all of this primary productivity that we've made, all of this photosynthesis, as we talked about, is the base of the food webs in all ecosystems.

And so we're going to start to dissect this. This is a marine food web showing phytoplankton that are eaten by zooplankton. We used to talk about food chains, but we well now that it's not a chain. It's really a very complex web and very hard to put organisms and assign them to particular sections. Phytoplankton are eaten by zooplankton. Zooplankton are eaten by worms. You've got blue crabs, barnacles, and the top predators shore birds and sea bass.

Now, an important part of these food webs is also all of the carbon, the primary productivity that is not eaten while it's alive. So some things just die, right? You have dead carbon lying around. And that dead carbon falls into what's called a different food web, the detritus food web. And we're going to talk about that. And it comes from all of these different components in the food web.

So now we're going to more analytically look at the flow of carbon. And when we talk about carbon we are also talking about energy, right? Carbon and energy are the same thing. I mean they're interconvertible. So we're going to look at the flow of carbon from the phytoplankton to the zooplankton through that trophic level. And to do this we have to talk about some definitions.

And again this is in your handout so I'm not going to write all this on the board but we'll just walk through this. The flow of carbon or energy through a trophic level, which is one of these links, OK? This is one trophic level. This is the next trophic level. Or you can also think of this as an organism. This type of analysis applies to both. And we start out with the productivity at trophic level and minus one, OK? And so the first would be primary productivity coming into the system.

Some of that productivity, some of that carbon is not ingested by the next trophic level. That's lost as dead organic matter, detritus, whatever we want to call it. So that's D_{n-1} the portion not consumed. Then some of it is ingested by the organism, I_n . And then some fraction of that is assimilated by the organism. That means it's taken into its biochemistry and goes toward building biomass.

And some of it is lost as fecal matter produced, that's F_{n-1} . And urine would also be a part of this, waste products. And then some of it is then, the rest of it is then available, oh, some of it, this is important, is lost as respiration. And then the rest is available as productivity for the next trophic level. OK. So different types of organisms. First, before we get to that, using this analysis we can start to define efficiencies of energy conversion through this system.

And this is because different types of organisms assimilate carbon with different efficiencies. And that is important in the flow of carbon through different types of ecosystems. So let's look at the first efficiency that would be I , ingested, reflecting the amount that's ingested relative to the amount that's available. And this is called the exploitation efficiency, OK? I_{n-1} divided by P_{n-1} .

The next one similarly would be A_{n-1} , the amount that's assimilated relative to the amount that's ingested. And that is the assimilation efficiency. And finally the amount that goes to the next trophic level divided by the amount that's assimilated, which is the production efficiency, the amount that actually goes to productivity that is assimilated. And these all multiplied together give you the ecological efficiency.

And that is sometimes called the trophic transfer efficiency. That's the amount of carbon that is basically lost as you go through one trophic level. And usually, and we'll talk about this in a minute, this is 10% to 20% actually makes it through the system, and the rest is lost to respiration or detritus or fecal matter. OK, so let's talk about now how different organisms vary in terms of efficiencies.

We have, in terms of the exploitation efficiency, if you're talking about, for example, tree insects. So insects feeding on trees is about 1% to 10%. They don't take that much of the tree. If it's grass to animals it's more like 20%. And if it's phytoplankton to zooplankton it's more like 20% to 40%. In other words, zooplankton harvests much of the primary productivity, no, almost half of the productivity that the phytoplankton have made.

OK. What about assimilation efficiency? How does this vary between organisms? Well, this one, you can think about it as if you eat food that is, I was going to say not you, but it is true, we are all animals so it applies to us, too. If you eat food that is similar in composition to your own bodily composition you're more efficient at assimilating it because you don't have to break it down as much and reorganize it.

So herbivores, organisms that eat plant matter are 20% to 50% efficient in their assimilation. But carnivores is more like 80%. Because you are meat and if you eat meat you don't have as much waste than if you eat a lot of fiber. So there are big differences there. And then in terms of, that is not a value judgment on whether you should eat meat or not. I just want to make that very clear. What? OK. But later on we'll talk about the difference between eating meat globally and being vegetarians in terms of utilizing primary productivity on the earth.

But in terms of production efficiency you have warm-blooded organisms having a 2% production efficiency. Whereas cold-blooded have a 40% production efficiency. Why would that be? Yes. If you're warm-blooded, does anybody know the technical term for that? It is if you are homeotherm. Or what did you say? Endothermic. I'm not sure. I think that's chemistry.

It sounded good, though. So there are homeotherms and heterotherms. It doesn't matter. The point is that these have to maintain their body temperature like we do. That takes a lot of energy. Whereas, these go with the flow so to speak, that technical term. But that doesn't take as much energy. If it's cold they just let their body get cold. They don't burn, burn, burn to keep the temperature constant.

OK, so that's how organisms differ. Now let's move on to the next chapter in which now we are going to look at -- We were looking at the flow through one trophic level. Now we're going to connect a whole bunch of trophic levels. We're going to look at the flow of energy through this component of this food web and do a more thorough analysis. OK, so this gets kind of messy but let's start here.

I better use the powerful one. OK, so each one of these is what we call a trophic level. And these are the primary producers, the photosynthetic organisms. Here is our gross primary production absorbing sunlight. Some of that is lost to heat. Some of that is lost to respiration. Here is our little $R_{sub A}$, remember? Right here. And some of it, the net primary productivity is available for ingestion at the next trophic level which are the herbivores.

So all we're doing here is ganging up a whole bunch of those individual analyses. And then the next trophic levels are the carnivores and then the second carnivores. And the number of links you have here is something that is obviously determined by the efficiency of transfer from one to another and the total amount of energy that comes into the system.

So here in our ecosystem we have carbon being lost at each step to detritus. And you have feces at each link. This all goes down and becomes part of the detritus food web. And in that you have two forms of carbon. You have particulate organic carbon which is pieces of dead carbon floating around, dead leaves, dead phytoplankton, whatever. And then you also have dissolved organic carbon.

When these plants die and the phytoplankton die they burst open. And the glucose and amino acids and all of that dissolve into the water in the system. And that

becomes dissolved organic carbon which is available for this microbial food web, an entirely different food web that's coupled to the system. So you have the detritivore. This the grazing food web here. The waste from that goes to the detritivores and the microbes.

And then whatever is left over after that is called refractory carbon. That means none of the creatures are able to break it open and really get energy out of it. And in the big picture what is this? We talked about it actually last time. Fossil fuel, exactly. This is the carbon that actually accumulates over time that when ecosystems are finished processing all of the primary production.

OK, so I'm trying to time this right so that we make sure we have time for the movie. So let's look at a couple of ways we can think about this. Let's just compare. If we look at the open ocean ecosystem versus the tropical forest. And the average, oh, I forgot one thing. OK. If we take now the gross primary productivity. And I'm going to circle all of the respirations. See the purple here? So this is all the carbon that's being fixed.

This is that is lost to respiration. And we can define a new parameter which is net ecosystem production. And that is gross primary production minus the respiration of all of the autotrophs, $R_{sub A}$, minus the respiration of all of the heterotrophic components of the system. So that would be the herbivores, carnivores, detritivores, microorganisms. That's all the carbon that's respired and lost to CO₂.

So you can add this to this. So we'd have net ecosystem production. Production equals GPP minus RA minus the sum of all the heterotrophs. Now, in very mature ecosystems this net ecosystem production is essentially nothing. All right? Everything that's produced is consumed. For example, in a tropical rainforest you don't have a huge buildup of organic carbon in a tropical rainforest. Everything that's produced is basically consumed and this is zero.

But in a young forest, say a plantation at the extreme where you plant trees and they're increasing in biomass, then obviously this net ecosystem production is a positive number. What if net ecosystem production is a negative number? It won't be there for long, right? You've got to have things photosynthesizing net at least enough to maintain the ecosystem. I mean you can have it for a transient for not any steady state.

OK. All right. Talking about ecological efficiencies again. If we talk about the average -- The average ecological efficiency of the open ocean is about 25% and of the tropical rain forest is about 5%. So the average number of trophic levels, that's basically the number of links in the food web in these two systems is about 7.1 and 3.2. In other words, when you have more efficiency of transfer from one link to another you can have more links obviously.

So getting back to humans again, and this gets back to in terms of what we might think about as a global human society. If you go from wheat to man you lose 90% of the energy in that transfer. If you go from wheat to cows to man you lose 90% here and you lose 90% here. So obviously in terms of feeding the world it's much better to go directly from wheat to humans than to go from wheat to cows to humans.

You all know this but it's important to remember that. And unfortunately the trend in the world is to go more from here to here instead of the other way around. Just

something to remember in terms of the application of this knowledge. OK. Finally very quickly I'm going to skip over this and go to another way to look at what we've been talking about.

It's just another diagram of the same thing. You have the photosynthetic organisms that the entire world depends on, this productivity for food and fiber. And that most of that is lost through respiration and the rest goes to the other organisms including detritivores. So a big question is how much of this global primary productivity, this global photosynthesis have humans taken over? It's really hard to answer that question, OK, but a lot of ecologists have been working very hard at understanding the fraction of global photosynthesis that has been what's called co-opted by humans.

And the estimates range from 10% to 55%. The amount that we use directly as food or fuel or fiber or timber is not that great, but there's a lot of productivity that's diverted as crop waste, burning, et cetera. And land conversion obviously uses up a lot of habitat and productivity. So the significant point here is that as we co-opt this primary productivity we change dramatically all of the food webs that rely on it, and that is what is part of the path to extinction of a lot of species.

And the big question is how much can we co-opt? I mean we're on the road to taking over the primary productivity of the earth, there's no question, completely. Unless we set up reserves that's it, that's where we're marching. Now, when we're in charge of it, is it going to function the way we need it to function to maintain our atmosphere and to provide us with the food and fiber that we need? That's still an open question.

OK, so now I'm going to show you this really neat DVD because these pictures of food webs are deadly dull and don't represent anything at all of what the reality is like. So I'm going to show you three weeks in the life of a real food web. And I want you to think about two things when you're watching it. Don't just think you're at home in front of your TV watching a nature show and going brain dead or something.

Think about what you've learned in this class. So think about the gigatons of carbon that are flowing through this system. More importantly this entire food web and everything that's going on in it is orchestrated by the information in the genes of the organisms in the food web. That's the information content that structures this whole thing. And how it's all orchestrated and coordinated and happens the same way more or less every year is absolutely mind blowing as far as I'm concern and a major, major challenge for ecology and for molecular ecology.

OK.