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CONTENTS:

Warming of the World Ocean

Introduction:

The world ocean has warmed. Global sea surface temperatures for the last 100 years show two distinct warming periods: one from 1920 to 1940 followed by a period of cooling, and a second period of warming from 1970 to the present. On average, temperatures of both surface and deep ocean water have increased during the last thirty years by 0.3 degrees Celsius.

The ocean drives the Earth's climate system. The movement of warm water from the tropics towards the poles causes the ocean currents and weather patterns we are familiar with. An understanding of how the ocean stores and transports heat is necessary to understand, model, and predict how the Earth climate system will behave.

Newly available information reported in *Science* magazine indicates the world ocean system has warmed substantially in the last fifty years[1]. How much of the observed heat increase is due to natural variability and how much due to our pumping greenhouse gases into the atmosphere is not known. The observed warming of the ocean is consistent with the idea that the warming of the entire Earth climate system, including the ocean, the atmosphere, and the cryosphere is due not to natural variability but more likely caused by fossil fuel-generated greenhouse gases entering the atmosphere. We spoke with Sydney Levitus about his work in documenting the increase in the oceans' temperature.

ER: Mr. Levitus, what is your scientific background?

SL: I became interested in the study of the ocean when I took a course in earth science as a freshman in high school. Within about a year of taking the course I decided that I'd like to try a career in oceanography. I wasn't completely sure what oceanography was about but I investigated various universities and read up about it and decided to major in it as an undergraduate. So I went to the New York University School of Engineering and Science and majored in oceanography and meteorology as an undergraduate.

Then I went to graduate school, also at New York University and I received a Masters degree in physical oceanography there. I started my graduate studies working with a numerical ocean modeler, and although I learned a great deal in the two years that I was in graduate school, I decided that rather than numerical modeling I wanted to work with data. I had taken courses on the general circulation of the ocean and atmosphere and read books about the Earth's atmospheric climate, and felt I wanted to do something similar for the oceans.

I was surprised to find out how little work had been done in mapping the oceans, and when I left graduate school I went to work for NOAA and fortunately got a position at the NOAA Geographical Fluid Dynamics Laboratory in Princeton, New Jersey. They pioneered the whole field of general circulation modeling of the atmosphere and ocean. I was in the observational studies group and began working with oceanographic data there, and I've been doing it for the last twenty-five years.

I took the oceanographic data and developed a climatological atlas, a digital atlas, and published that in 1982, and that atlas has had a lot of utility in the field of oceanography and climate research. It has been used in different ways, such as to verify computer simulations of the ocean and climate; and to provide initial conditions and boundary conditions for ocean circulation models and atmospheric models.

ER: What is a digital atlas?

SL: Well, most atlases until then had been hand drawn, but I used mathematical techniques to display the data on a one-degree latitude/longitude grid at various standard depth levels in the ocean. The atlas was distributed both as a set of maps but also on magnetic tape. It was distributed all around the worldm with no restrictions. Apparently the atlas served a need in the ocean and climate research communities because it's been cited quite heavily over the last eighteen years.

I spent the first fifteen years of my career developing these climatologies and ocean databases, and doing quality control of the data. Then in 1989 I published a series of papers that described the variability of the North Atlantic ocean and I documented that there were changes in temperature and salinity on gyre and basin scales in the North Atlantic. Those papers have been cited a large number times. But we had run out of data; there wasn't much more data than I had to work with at the time for doing these studies.

ER: What sort of information would go into the atlas?

SL: What we are particularly interested in is knowing the variability of temperature and salinity in the world ocean. These two variables determine the density of sea water, and changes in them can reflect changes in the circulation of the ocean.

The Earth's climate system is composed of the atmosphere, the ocean, the cryosphere and the biosphere.

ER: What is the cryosphere?

SL: The cryosphere is sea ice and land ice.

So anyway, the Earth's climate system can't be looked at as just the atmospheric climate, in includes these other components, it is the Earth system. For many years scientists had speculated that the ocean is the memory of the Earth's climate system because of its large mass and high specific heat. This is why it's important to have historical data on the variability of the ocean as we try to describe changes in its temperature-salinity structure, and try to understand the physics involved.

ER: Why is salinity important?

SL: Salinity is important because it not only partly determines the density of sea water but it is related to the Earth's hydrological cycle. If there is increased rain in a certain area, then salinity will go down. If you get increased evaporation, salinity will increase; if you increase salinity at the surface, the water may become dense enough to sink.

ER: What is the connection between the ocean and the climate?

SL: To understand the Earth's climate system, we have to understand the ocean. The ocean and the atmosphere transport heat from the tropics to the poles. In the tropics of the Earth's climate system more heat is absorbed than is given back off to space, and in the polar regions more heat is radiated back out to space than is absorbed. So in order for the Earth's climate system not to develop huge gradients in temperature between the tropics and poles, there has to be a transport of heat from the tropics to the poles. This is one of the main things we're trying to understand: how does the Earth's climate system maintain the stability of the equator to pole temperature gradient? Or if the gradient is chang-

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ing, how does it change and what are the mechanisms?

ER: What is an example of such a mechanism?

SL: One of the things that can happen is that if you cool an area of the ocean and the water sinks, it can after sinking be transported pretty large distances and can remain away from the sea surface and away from contact with the atmosphere for years or decades or centuries or millennia. For many years it has been thought possible that the ocean could basically sequester heat, keep it away from the atmosphere, and you might see a cooling of the atmosphere after that happens.

This brings us into our present work. Over the last seven years I've led an international project called the Global Oceanographic Data Archeology and Research Project. It's a United Nations sponsored project of the Intergovernmental Oceanographic Commission.

Scientists were aware that there was a great deal of historical oceanographic data that had been collected but had been handwritten and had never been digitized. The goal of the project was to locate as much of these historical data as possible and to digitize them. Over the last seven years we've located and digitized about 2 million temperature profiles and many other types of profiles — salinity, oxygen, chlorophyll and other variables — and we've put these into an integrated database that we've distributed on CD ROM and that we also make available online.

ER: What did you learn from that project?

SL: Our most recent study, which was published in *Science*, documents the fact that there is substantial decadal variability in the heat content of the world ocean, and that over the last thirty-five years the ocean has undergone a considerable warming. Even though the magnitude of the temperature increase — which was about one-tenth degree Fahrenheit averaged over the upper 10,000 feet of the ocean — may seem like a small number, in fact it represents a huge increase in the heat content of the world ocean.

For the last ten years critics of the results from models that simulate the effect of increasing carbon dioxide in the Earth's atmospheric climate were saying that we're not seeing in nature as large a temperature increase in the atmosphere as the numerical simulations predicted. The response of the climate modelers was that they believe that a lot of the heat was going into the ocean, but at that time their models didn't have an ocean and so the atmosphere showed this larger warming than was observed. Our results show that the ocean has warmed; the magnitude of the warming is consistent with the increase in heat that was predicted through these early climate simulations with increasing greenhouse gases.

To understand the Earth's climate system we have to understand the ocean.

While this isn't definitive proof that increasing greenhouse gas has affected climate, it's another strong piece of evidence that this is what is occurring. But we also see strong decadal variability of heat content in the ocean, and this has us puzzled. It's a completely surprising result.

ER: Do we know what the natural variability is?

SL: This is the first time we've computed this quantity for the upper 3,000 meters of the world ocean. The question is, critics will say, Do you have enough data? and I believe we do. We first published our results a few years ago but didn't publicize them. We had a million fewer temperature profiles, when we first published these results as part of a NOAA atlas. We've added an additional million profiles, and we still see these same general features. We continue to add data, particularly data to areas such as the Southern Hemisphere, which are relatively data sparse.

We're also working with computer modelers to see what the rate of increase in heat content is from their simulations, and we will be publishing a paper shortly describing the results of their computations, plus changes in atmospheric heat content during the past fifty years. So this is the beginning of, I think, a decade where we're going to be looking at the climate system in a somewhat different way; that is, looking at the total heat content of the system and how that changes with increasing greenhouse gases.

So, yes, there will be criticism, but that's part of science. The fact is that, if you look at all the evidence, I think there's a strong case being made: there's no question now that the atmosphere has warmed over the last hundred years, at least surface temperatures have warmed.

ER: Its pretty much accepted in the scientific community that the climate system has warmed. The issue is whether it is due to natural variablity or a greenhouse effect.

SL: When you look at all the results: paleoclimatic data, proxy data, for temperatures such as temperatures inferred from tree rings, and those show that over the last thousand years there's been no warming even comparable to the warming that's occurred in the last hundred years. Personally I believe that's some of the strongest evidence for the fact that we are seeing an increased warming due to greenhouse gases.

There are many other pieces of evidence I could cite, but the Intergovernmental Program on Climate Change will be putting out the definitive study next year on the state of the Earth's climate system. Based on their preliminary announcements, it's clear that the consensus is that the Earth's climate system has warmed and part of this warming is due to increasing greenhouse gases. It's true there is substantial decadal variability, but all the evidence points to a large human influence.

ER: What are you going to do next?

SL: We're now working with the modelers, supplying data and products to scientists around the world, and we continue to work with various institutes and countries from around the world to build databases as well. The databases are available internationally without restriction, and scientists who want to use the data have it basically without any problems. We have a strong belief in making all the data we work with available.

ER: You said the ocean is the memory of the climate. I've thought of it more as a buffer or a flywheel, a moderating influence on things.

SL: The ocean provides a long-term memory. It's a different way of saying that the ocean is the flywheel of the system. What we're seeing in our results is that there are these decadal variations and longer term. But we only have thirty-five years of data, so when we compare it with changes in atmospheric heat content, for example, we're seeing that the change in ocean heat content over the last forty years is twenty times larger than what we see for the atmospheric heat content. That clearly indicates that the ocean is the major player in the Earth's climate system in terms of storing heat.

... the magnitude of the ocean warming is consistent with the increase in heat that was predicted by early climate simulations with increasing greenhouse gases.

ER: Well, how many joules are there in the ocean and how many are there in the atmosphere? It would seem to me the mass of the flywheel is in the ocean.

SL: Yes, that's what I'm saying. We gave the numbers in our paper, but the range of heat content from 1955 to 1995 was $20x10^{22}$ joules, and the interdecadal change of atmospheric heat content is a factor of 20 smaller, and so that means that the ocean is playing the major role.

But nonetheless, based on other studies we know that the atmosphere can transport as much heat from the tropics to the poles at some latitudes as the ocean does. So we have a situation where both fluids are working together, and that's what we need to understand in order to make decadal forecasts about climate. Part of our work has been quantifying and showing that the ocean is the memory of the Earth's climate system. We have the numbers to show it, and the numbers indicate that there is a possibility of decadal prediction. If we know that a great deal of heat is being taken out of one part of the ocean and put into another part of the ocean, there is a possibility of forecasting climate on decadal time scales.

This is the subject of an international research program called CLIVAR which stands for *Climate Variability and Prediction*. It's a program of the World Climate Research Program. CLIVAR has the goal of trying to understand the variability of the Earth's climate system on decade to century time scales. The CLIVAR program has recognized since its inception a few years ago that the ocean must play a large role in this process.

ER: What would a decadal forecast look like?

SL: Well, it might be a forecast that said over the next decade we can expect that we'll have less rain in a particular region than we did in the past ten years. For example in the Sahel we know there's been a decrease in rainfall until fairly recently. I'm not sure whether the system is totally recovering but if you look at rainfall estimates from the Sahel region in Africa, you can see that rainfall was decreasing and they had massive droughts that produced a tremendous amount of human suffering.

The droughts are related to changes in sea surface temperature, which may be related to changes in atmospheric circulation. So we may be able to produce forecasts that say we're going into a period when we're going to see increased droughts in the Sahel or in the Midwest of the United States. It may be that we would expect three out of ten years to be normal and seven out of ten to have much less rain than normal. It would be a very general type of forecast.

But just as we've started making successful predictions of El Niño in the last several years, we hope to be able to predict climate on decadal time scales, and also to predict what will happen as greenhouse gases keep accumulating in the atmosphere.

ER: What will be the consequences of increasing greenhouse gases?Are we any closer to a synthesis on that?

SL: This is another subject that's going to continue to be heavily studied during the next ten years: what are the sources and sinks of carbon in the Earth's climate system. The ocean can be a considerable source or sink because sea life such as some plankton use carbon dioxide to create their shells, which are made out of calcium carbonate. When plankton sink, part of their population sinks to the sea floor and form sedimentary layers. This effectively removes carbon dioxide from the climate system for tens of thousands of years and longer. Part of the population are recycled in the water column by dissolution with the calcium carbonate being used by other plankton. So we have to understand any changes in ocean conditions that might lead to changes in the amount of plankton being formed. But there are also sources and sinks of carbon on land; these are going to be major sources of research during the coming ten years.

The US Global Change Program will in part be focusing on ecosystem response to climate change. Ten years ago there was a lot of skepticism attached to whether the Earth's atmosphere was even warming. Now it's widely accepted that the surface air temperature and sea surface temperatures have warmed on average. Regardless of what part of this warming is due to increasing carbon dioxide and what part is due to natural variability, we still have to learn to manage these changes. If this were natural variability and we're still seeing large increases, it's still an important phenomenon to try to understand.

ER: Have there been any ill effects of having a warmer ocean so far?

SL: There are indications that coral reefs are being stressed by increased temperatures, although there may be other factors involved such as minerals being deposited in the ocean from dust storms off the Sahara. So with all these complicated issues, the ocean may be playing a major role and we have to understand how the whole climate system operates, including the biology and the chemistry.

ER: In genereal, is climate change going to be a good thing or a bad thing?

SL: Some of the effects are good. In some areas the diurnal surface temperature range has decreased and it's made for a longer growing season. This is one of the predictions that's been made that's associated with increasing greenhouse gases. So some areas may benefit.

Some areas may be hurt in terms of their suitability for growing crops. Fisheries are affected because if the ocean circulation changes and atmospheric circulation changes, then fish may migrate or it may become difficult for them to sustain populations in some areas. Since there are already problems with overfishing, if the fisheries are subject to climate change stress as well, we may not see a recovery of some of the fisheries, such as the cod fishery of Newfoundland.

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Climate has a direct impact on production of food and how we lead our lives. A large percent of the U.S. population lives in coastal regions, and those regions can be stressed by increasing pollution. What if a region were to become more stagnant because of the change in atmosphere or ocean circulation?

If some of these areas warmed, as we know has happened off the coasts of South America, Bangladesh, and India, then you can expect an increase in the outbreaks of cholera since cholera is now known to live in certain zooplankton. If temperatures are warm enough, there can be a zooplankton bloom and an increase in the bacteria that cause cholera. If a region has adequate water treatment facilities, then we can perhaps not worry about cholera, but if we don't have adequate treatment facilities for water, then we may be facing increased outbreaks of cholera. During the last El Niño there was an increase of cholera in some regions because of the increase in temperatures in some coastal areas.

ER: It is a warm weather disease and we didn't understand that until fairly recently.

SL: Right. Yes, it was the present Director of the National Science Foundation, Rita Caldwell, with her colleagues, who found where the source of the cholera bacteria are and that it lives in the ocean in a form that is dormant until certain conditions are ripe for the development of the plankton and the bacteria.

ER: Aren't some parts of the ocean actually cooling?

SL: Yes. Although there's been a net warming and it's consistent from what we expect from an increase in greenhouse gases, we've never implied that the ocean is warming by the same amount in each place. In fact, in the sub-Arctic of the North Atlantic — between 45 North and 65 North — that region has been cooling. The upper ocean has cooled since the late 1940s, and the deep ocean, particularly in the Labrador Sea, began cooling in 1971. That means that that region of the ocean has been giving heat off to the atmosphere.

So we have an interesting situation: even though the North Atlantic has warmed on average during the past 45 years, parts of it have been cooling down while the rest has been warming in such a way as to make the net temperature change positive for the North Atlantic. The cooling of the sub-Arctic in the North Atlantic may be affecting the cod fishery there, for example. We're also seeing a cooling in parts of the North Pacific which likely is affecting salmon fisheries in this ocean.

So ocean warming can have local impacts, but the scientific community is still trying to sort a lot of this out. To bring in all of the different facets of the climate system is a considerable intellectual undertaking. In the scientific community, we don't really have generalists with respect to the climate system so much as we have a lot of experts, and so we're trying to bring all the different facets of climate and climate change together, and especially through the IPCC to produce a report that summarizes the changes that are occurring and what could occur in the future.

ER: The IPCC is an intellectual juggernaut. The people who are in denial about climate are faced with this overwhelming scientific consensus.

SL: Yes. I think now they acknowledge there's been a warming, but they're saying, Well, okay, but we're still not sure what's causing it. They are a small minority of the scientific community. When you look at data like bore hole temperatures, they indicate that there's been a warming around the world over the last several hundred years. We've seen that the ocean's undergone a net warming consistent with increase in heat content predicted from the models. We see the lower atmosphere has warmed. We see from paleoclimatic data such as tree rings and lake sediments that there has been a warming. All of this evidence taken together I think is compelling. That will be summarized and published by the IPCC next year.

There's no question now that the atmosphere has warmed over the last hundred years ...

ER: Do you understand what's going on with the cooling of the North Atlantic and North Pacific?

SL: We have a rudimentary understanding but realize that it's only been in the last ten years that we've put together a lot of the data so we can begin to understand these phenomena. Approximately twenty-five years ago the large-scale atmospheric circulation patterns, particularly as shown by sea level pressure, have shifted into a state that's producing changes that result in warming in some regions and cooling in others for both the atmosphere and ocean. The question stll is, how much is this due to natural variability how much is due to the observed increase in greenhouse gases?

The Earth's atmosphere and ocean may have certain modes of variability, certain patterns that they can get locked into due to forcing, and as patterns change, there is an associated change in storm tracks. We know that the storm tracks in the Atlantic Ocean change with respect to the North Atlantic Oscillation in sea level pressure. Since about 1971 the storm tracks have changed and we're getting many storms that track across the Labrador Sea. There's been a tremendous heat loss from the Labrador Sea, which shows up as this tremendous cooling. Even from the surface down to about 2,000 meters depth, the Labrador has cooled by about one degree Celsius, and it's also gotten fresher. We have never seen water this cold there, and this water is now spreading in the deep layers of the North Atlantic.

We know that since the Labrador Sea has been cooling down, heat has been given off to the atmosphere, and that's probably had an impact on the atmospheric circulation. But will it be a positive or negative feedback? Will the increasing heat to the atmosphere in the Labrador Sea eventually force another shift so that it will go back to another change in storm tracks and we won't get this cooling in the Labrador Sea because the storms are now somewhere else? These are the types of things that we are trying to understand.

We know that you can change the ocean's circulation dramatically based on these fluxes of heat and fresh water from the ocean to the atmosphere. Many people think this is a slow process, but in fact geologically speaking, it's not slow. One of the things we've learned from studying ice cores and ocean sediments is that in the past the atmosphere and ocean circulations have changed on time scales as short as ten years. So the concern is that by increasing greenhouse gases we may shift the climate system rather abruptly, so abruptly we wouldn't have time to mitigate.

I may have gotten a little bit away from your initial question, which was to talk about the cooling of the sub-Arctic, but it's an example of how complicated the system is. And there are still many things we don't understand. But the point of our work is that there has been a net warming of the world ocean and there are changes occurring on decadal time scales. This is something that we need to understand much more.

...over the last thousand years there's been no warming even comparable to the warming that's occurred in the last hundred years.

ER: There is a conveyor system of heat in the North Atlantic from the tropics, of deep water; I don't know what it's technically called.

SL: Scientifically we call it the thermohaline circulation, and what I was describing is part of this. When you have convection in the Labrador Sea; that is, you have sinking, and tremendous losses of heat to the atmosphere during storms, the surface water is cooled and it sinks, then it's transported south while the upper layers of the North Atlantic are transporting heat in the form of warm water from the tropics to the polar regions. That's where the idea of the conveyor belt comes in.

ER: Has that conveyor shifted or changed directions in the past?

SL: Yes. We know from the geological records that during the last Ice Age that the ocean circulation was very different. In fact the Gulf Stream left Cape Hatteras and extended almost due east rather than going towards the northeast and warming the UK and other regions of northwest Europe. Such a circulation change now could have big impacts on our climate.

ER: Are we closer to tripping that conveyor reversal? Are we talking about that much heat transfer, or do we even know?

SL: Well, this is one of the possibilities that we have to look into because we've increased carbon dioxide by 30 percent over the last one hundred years, and I believe the carbon dioxide levels in the atmosphere are now as high as they've been at any time during the past 160,000 years. As scientists have pointed out, we are conducting a big geophysical experiment. We can't say for sure, but one of the possibilities is that we could go into an abrupt climate shift. If we were to, there's little question the ocean would be involved. Our instrumental data though are only for the last fifty years for the ocean, and so it's hard for us to talk based on the instrumental data as to what might happen. We know what's occurring now in some areas, but not in all areas. But we know from the paleoclimatic data that there have been these big shifts.

And yes, there is no question that I think many scientists are concerned we could flip into a different climate space because we've increased the amount of carbon dioxide. The fact of the matter is that not only has the ocean warmed in the lower atmosphere, but sea ice has decreased in thickness by about 30-40 percent over the last thirty years, and this has been a surprising result.

ER: This is fairly new information, isn't it?

SL: Yes. The study was published within the last year, and that was published by Drew Rothrock at the University of Washington based on declassified data from the U.S. and British nuclear submarines that patrolled in the Arctic. A decrease of 30 percent or 40 percent in sea ice thickness is pretty large. That's another piece of evidence that the climate system has warmed during the past forty years.

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What Good Is Biodiversity?

Introduction:

There are hundreds of different kinds of birds in the tropics but less than one hundred bird species in an equivalent area of North America. The same holds true for all kinds of life. If you count the number of species of insects or plants or snails, you will find a bigger number in the tropics than in higher latitudes. It is not known why this is so, but that doesn't stop ecologists from arguing about it.

One common explanation is that more productive places will support a larger number of species. In ecological parlance, primary productivity refers to the amount of plant growth; that is, an acre with twenty tons of plants is more productive than an acre with only ten tons. So the idea goes that more productivity can support a greater variety of animals, plants, bugs and fungi.

With the unprecedented growth of the human population there are few places left on the Earth, land or sea, that have their full complement of life forms. There are about 10 million different life forms on the Earth; half of them may well be extinct in 100 years, primarily because of human conversion of their habitat.

What will be the consequences of this biological holocaust to people? We rely on our ecosystems to provide clean air, water, food, shelter, and fuel. Clearly, ecosystems cannot perform these services as well as they can if half their life forms have disappeared. Thus what would be an academic, theoretical debate among scientists about the effects of biological diversity on ecosystem function has become an argument with serious implications for our future. In crude terms the question is, how much damage can we inflict on ecosystems before they stop functioning?

> Maintaining a diverse portfolio of species or a diverse portfolio of stocks increases the chances that you will see less fluctuation in the total because as some do poorly others may do better.

We spoke with Michael Huston about this somewhat arcane but very important debate.

ER: Professor Huston, what is your training?

MH: I attended Deep Springs College and then I received a B.A. in biology from Grinnell College, and a Ph.D. from the University of Michigan. My Ph.D. was on the effects of environmental conditions on early succession and tropic rainforests. I pretty much directly came to Oak Ridge from the University of Michigan.

ER: In what capacity do you work at Oak Ridge?

MH: I'm a Senior Scientist in the Environmental Sciences Division. I work on issues related to the environmental effects of energy technology, which includes things like acid rain and climate change. Much of my work is focused on basic ecosystem processes at a research site here called the Walker Branch Watershed: long-term studies of hydrology, nutrient cycling, forest dynamics. I've been involved in all of that.

ER: What is Oak Ridge National Lab?

MH: Oak Ridge is a multipurpose laboratory that in addition to nuclear physics, addresses issues of material science, advanced ceramics, parallel computing, and climate modeling. It's a much more diversified place than, say, Los Alamos or Sandia. Oak Ridge National Lab is minimally involved in military and weapons work, although there is another plant in Oak Ridge that's not official laboratory that is involved in that, although it's mainly disassembly and storage now.

ER: Can you give us a little background information about this controversy?

MH: Sure. There is a long history of observations that the numbers and types of species – both plants and animals – change dramatically from one part of the Earth to another. You can compare the number of different tree species in Wisconsin to the number of different trees in an equivalent area of Brazil and see huge differences. There are things that change between Wisconsin and Brazil: the fact that one place has winter, the other doesn't; the types of biological processes that seem to be important, and the rates at which those processes occur.

For a long time these observations were linked with the idea that environmental conditions influenced the number of species that one found in a particular area. This gave rise to many different hypotheses dealing with the question of species diversity. Then a subsequent question is how do those species coexist, and why do you find more species coexisting in one place than another?

Many different ideas have been proposed about what aspects of the environment and climate influenced the number of species. One idea was that stable climates — places without winter and severe conditions — allowed more species to evolve and then to survive because they weren't subjected to winter.

Another idea is that in a more productive environment, one in which there was more food or conditions were better, you could have more species because they could divide the resources up in a way that would allow more species to coexist.

All of these explanations were based on direct observations about the number of species found in different places and assumptions or deductions about the quality of the environment.

There is the assumption that tropical ecosystems are more stable than temperate or boreal systems, which now I think we realize is not necessarily the case. Severe droughts, fires, hurricanes, those sorts of things occur in the tropics and they have effects that might be analogous to winters or perhaps even glaciation in the higher latitudes.

> I think most ecologists on both sides of the issue are coming to the consensus that in most situations it's not the number of species in a community that is important but the properties of the individual species.

ER: Is the amount of biomass greater in the tropics, or is it just the number of species?

MH: I'm afraid that we don't have an answer for that.

ER: The difference in the number of species between high and low latitudes is orders of magnitude. Apparently the difference in biomass is not so obvious.

MH: The difference in species between the latitudes is easy to observe and we're all impressed by tropical rainforests, which do have some pretty big trees. But there are a number of problems in interpreting what's going on, and one of which is that most of the temperate ecosystems have been severely impacted by man. Most of the forests in Wisconsin were cut 100 or 150 years ago. As best as we can tell, they had some huge trees, trees that were probably as big as what you would find in tropical rainforests or perhaps bigger.

Comparing temperate forests now to tropical forests now is not necessarily a fair comparison. In general, if one goes to the remnants of temperate forests that we have that are least impacted, they have as much biomass as most tropical forests, and in many cases more. So more species in the tropics is not a matter of having more biomass necessarily, but we don't have good data on this, and we're currently not collecting good data on this. The last big effort to look at this question was back in the late 1960s and 1970s with the International Biological Program where people went out and measured these things. Since then, people have been working on ways of getting equivalent information from satellites, but we're still short on the ground truth.

There are two fundamental questions we can't yet answer. One is, what are the differences in biomass as it's distributed across the globe, particularly from temperate to tropical ecosystems? The other closely related issue is what is the difference in primary productivity; that is, the rate at which plants are taking up carbon and converting it to plant mass? And again, we have some information but not enough for an unequivocal answer. I think in general we could probably say that the amount of biomass doesn't differ all that much. There are a number of ways of looking at primary productivity, but as a generalization I think we could say it looks as if a tropical forest has about as much primary production in a year as a temperate forest does in its growing season of three or four months. On an annual basis there doesn't seem to be a huge difference.

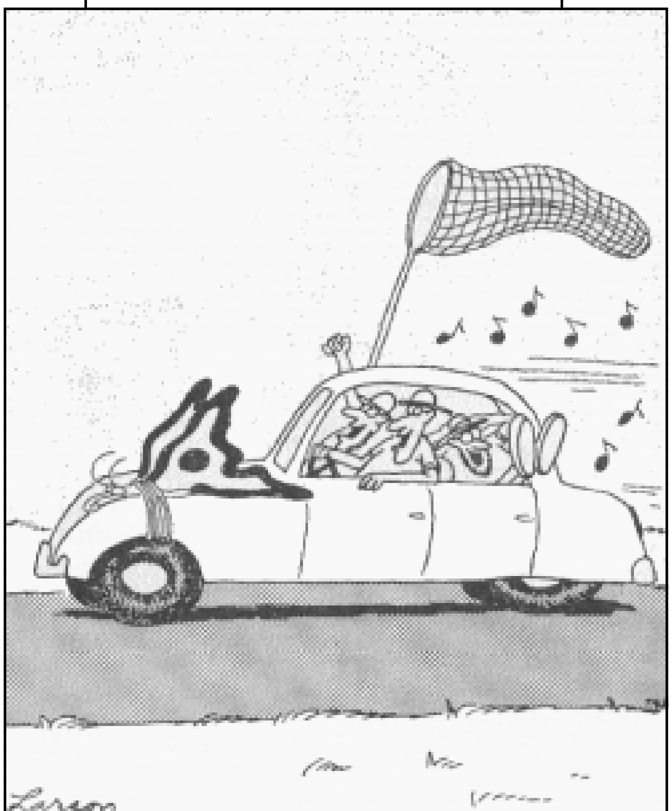
ER: I've always pictured tropical rainforests as the most productive places that can be.

MH: The assumption was that tropical forests were much more productive than temperate forests. This was ecological dogma, and it's a belief I think that's still held by many people, even though the evidence is not there, and there is as much contradictory evidence as there is supportive evidence. But that assumption was taken to be support for the idea that high-productivity environments tended to have higher species diversity.

The problem was that as people began to measure productivity more carefully, and particularly to manipulate productivity, and primarily in temperate ecosystems using fertilization experiments and looking at productivity gradients where you could actually get some decent measurements, what people have found is that the highest productivity environments don't necessarily have the highest plant diversity.

In general, plant diversity is highest in fairly low productivity environments, and as you go to higher productivity, diversity drops as a few species begin to dominate through competitive interactions.

The Far Side by Gary Larson



So to some extent the pattern is almost the opposite of what people thought it was, at least at some scales. So plant diversity increases from zero under conditions where plants can't live, to the highest diversity at fairly poor conditions of low productivity, and then drops as conditions get better and better and competitive interactions result in dominance by a few species.

ER: An example may be an old-growth forest in the Northwest. There's tons of wood there but not much diversity.

MH: That's certainly one example, and even in the eastern forests people often talk about the beech-maple climax. Whether or not you believe in climax forests, the general observation is that tree diversity goes down over the course of succession, so that in later succession you'll have domination by beech or maple or whatever is dominant in that particular region.

That sets up another concept related to the issue of diversity, which is the idea that disturbances that kill organisms, or in the forests, kill trees, prevent this competitive exclusion from occurring and allow more species to coexist. That is, periodic disturbances allow more species to coexist.

ER: Why has climax fallen out of favor? Every ecology course teaches the concept.

MH: I think we maybe questioned the idea a bit prematurely. I think that to some extent the climax was a concept based on the idea that there was a stable climate that led to a highly predictable and more or less constant endpoint of succession. I think that notion is gone out the window, mainly because paleoecological work has demonstrated that environmental conditions, climatic conditions change and we don't always see the same vegetation in the same location. So in that sense I think the climax concept has been modified.

However, the idea that you do get a development and change in vegetation through the course of succession is still very much alive and fundamental to ecology, and in that sense the climax as a term for the late successional state I think is still valid.

ER: Ecologists are a contentious lot but the argument about diversity being good for ecosystem function seems to be fairly heated even for them.

MH: The whole argument was framed in the context of what conditions influence diversity. Is diversity regulated by productivity, by stability, by disturbances? More recently, largely I think motivated by conservation concerns and in particular, concerns about issues of extinction, the question has arisen, What good is diversity? Does diversity serve a function? Can we justify the preservation of diversity because it is essential for some ecosystem properties? Essentially turning the old question on its head. This is a tricky area because we have a large body of information and a lot of theory and models that address the effect of productivity on diversity. We know that productivity is correlated with diversity.

When the question becomes, what effect does diversity have on productivity? we have to be careful to make sure we have the cause and effects going in the right direction. There's lots of evidence, many patterns of diversity in relation to productivity. The question is, to what extent can we interpret these patterns as the effects of diversity on productivity?

> ...for a given set of soil conditions and climate, do more species give you higher productivity or greater stability than fewer species?

To some extent I think there has been an active interest in demonstrating that diversity is good and diversity is important and there are scientific reasons that diversity must be preserved. The primary reason among them has become that diversity is important for productivity, which essentially is saying that higher diversity ecosystems are more productive than low diversity ecosystems.

Now, before we discuss the experiments, I think it's important to recognize that the patterns that we see in nature that I've already described, we find high diversity, typically high plant diversity, in unproductive environments and the most productive environments tend to have lower plant diversity.

ER: Is that true even in the tropics?

MH: In general that's true in the tropics, although again we don't have quite enough information. But in general the most productive tropical forests are certain riparian forests that tend to have fairly high biomass and lower diversity. The important thing to keep in mind about the tropics is that in general, the soils in the tropics are very poor as a result of the weathering processes that occur at higher rates under warm, wet conditions. So in general, tropical forests are growing under fairly unproductive conditions, at least in terms of the soil resources. But even within the tropics there are gradients and variation in productivity.

While there aren't many good direct measurements of productivity, there's a lot of information on tree diversity in relation to soil conditions, such as nutrient levels, that may be correlated with productivity, and most of those examples show the pattern that I have been describing. For example, some work on Costa Rican forests that was published back in the sixties shows that the forests with the highest number of tree species are found on soils with low levels of soil nutrients. If you go to soils with higher levels of these nutrients, you find fewer species. That same pattern is found in African forests and in Southeast Asian forests.

Those are things that I have detailed in my book and other publications and many people have commented on that[1]. So that pattern is pretty well known, and that does tell us something about the effect of diversity on productivity in that high diversity does not necessarily overcome limitations of the environment. Which brings us around to the other question: for a given set of soil and climate conditions, do more species give you higher productivity or greater stability than fewer species? That's basically where the controversy has arisen because a number of experiments have claimed to have demonstrated that treatments with more species are more productive than treatments with few species. This is where we get into the crux of a different issue. This involves the question of how to select species for use in an experiment, and how our selection process relates to the way species naturally come together in a wild plant community.

There's a fairly straightforward experimental approach that on first glance makes a lot of sense, and that is to randomly select plant species from a group, randomly draw combinations with different numbers of species, look at each species by itself and then in random sets of two, four, eight and so on. The idea is to create random assemblies with different numbers of species and observe how they perform. This has been the approach taken, and the most comprehensive experiments have addressed this issue. Typically these experiments find that if one takes the average of all the combinations of one species and then looks at the average of the combination of two species, up to all of the combinations of the highest number of species, the average productivity goes up, which seems to suggest that the more species you have, the better off you are.

However, when one begins to look at this information a little more carefully, one can also see that as you go to higher and higher numbers of species, you have a greater chance of having a particular single species or a particular set of species that have higher productivity, they either get bigger, grow faster, or you have a higher chance of selecting a legume that adds nitrogen to the system. So that in addition to the higher number of species, you're looking at a higher probability of having a particularly strong species. There's a real question about how one interprets these sorts of experimental results.

If one looks at the average of the single species plots with each species planted as a monoculture, clearly large species planted as a monoculture will produce a large amount of biomass, but species that are small in size planted in a monoculture, will only produce a small amount of biomass. So if we look at the monocultures we'll be adding small species to intermediate species to very large species and essentially coming out with some intermediate level as the average.

However, at the other end where we have all the species put together, what we usually see is that the largest species from the monoculture is often the largest species in the mixture, and in many cases the mixtures, even though ten species may have been planted in them, they will end up being dominated by a few species. So in one interpretation what you're seeing in many of these mixtures is the effect of one or two species that dominate the mixture.

If mixtures are better than monocultures, then the mixtures should have higher productivity than the most productive monoculture. In general, this is almost never the case.

The alternative interpretation is we're looking at the properties of individual species. If one looks at the monoculture and finds the species that has the highest productivity, one should compare the productivity of the most productive monoculture to the productivity of the most productive mixture to answer the question if our mixture is better.

The question is, are mixtures better than monocultures? If mixtures are better than monocultures, then the mixtures should have higher productivity than the most productive monoculture. In general, this is never the case. In almost all situations the most productive mixtures are equivalent to or less productive than the most productive monocultures.

There's a technical term for a phenomenon called over yielding, and this is something farmers, of course, are very interested in. If you can get higher productivity by planting two species together than by planting either one of them singly, the objective then is to get the highest productivity and plant those two species together.

There's been a tremendous amount of both theoretical and experimental work in agriculture looking at how to quantify over yielding, and basically it comes down to comparing the most productive monoculture to the mixtures. Over yielding can be easily achieved in certain ways. For example, by planting legumes with grasses — for example, a mix of soybeans and corn or beans and corn — the productivity of the mixture is often higher than the productivity of either of those alone, and that's a fairly well known phenomenon.

ER: What does the grass give the legume?

MH: The grass doesn't necessarily give the legume much of anything, but the grass grows so much better with the legume providing nitrogen, that in spite of the fact it might have a somewhat negative effect on the legume, the overall yield is still high.

ER: The mixture just boosts the one plant, not both.

MH: It's more of a boost to the one. So there are cases when over yielding occurs and is easy to understand. However, in most of the situations where the effect of diversity has been looked at, except where legumes were involved, there's basically no over yielding. The most productive monocultures yield as much as the most productive mixtures.

ER: I have to wonder how relevant these agricultural type studies are to tropical biodiversity.

MH: The question is whether random assembly is relevant to real ecosystems. Is the process of randomly combining species in an experiment and seeing some sort of diversity response, is that relevant to the effects of diversity we might see in naturally assembled groups of plants? Again, this is a topic where there is disagreement. I think most ecologists feel that natural communities are not randomly assembled. There's strong selection by the environment and what species occur under particular conditions. There are limitations on dispersal, some species are good dispersers, others poor dispersers. What we look at when we see a natural community is not a random subset, but a specific subset that is there more as a result of some interaction with the environment.

So given that most of the support for a positive effect of diversity on productivity comes from randomly assembled communities raises the question in many ecologists' minds of its relevance to natural communities. In addition, there's the issue of over yielding. Unless over yielding can be demonstrated, even in randomly assembled communities there's not convincing evidence that diversity has a positive effect on productivity.

There is the idea that if we can show that losing species will cause ecosystems to deteriorate, there will be a more compelling reason to conserve wild species.

The real question is not looking at the average response but looking at the maximum response. Farmers are always interested in the maximum response, and they do everything they can do to get that at any particular set of environmental conditions, and evaluating the effects of the number of species on productivity basically shows that there is no strong effect.

ER: Is productivity that important to an ecosystem?

MH: I think it's important to recognize there are other ways in which the number of species can have positive effects on ecosystem processes; many of these have to do with maintaining stability over time. Having a larger number of species increases the probability that there will be, for example, a species that may do well during warm years and other species will do well during cool years, and other species will do well during wet years or dry years. This has been called the portfolio effect. Maintaining a diverse portfolio of species or a diverse portfolio of stocks increases the chances that you will see less fluctuation in the total because as some do poorly others may do better. This is a potentially legitimate effect of diversity on an important ecosystem process, instability.

However, what we often see in nature is that environmental fluctuations are sufficiently extreme that most species respond the same way, so that during a dry year most species will do much more poorly, during a wet year most species may do much better. There may be some adjustment within the species, but not nearly enough to compensate for the effect of severe environmental conditions. But from the perspective of a farmer, getting a little bit of yield during a drought will be better than getting no yield.

I think most ecologists on both sides of the issue are coming to a consensus that in most situations it's not the number of species in a community that is important but the properties of the individual species. Whether you have a grass and a legume is much more important than how many species of grass or how many species of legume you have.

To some extent this has been phrased in terms of functional types. There are certain functional types of plants that when grown together have higher productivity or may lead to a more stable productivity over an annual cycle or over multiple years. In general it's not the number of species but the particular mix one sees.

ER: Would having more biodiversity make extinctions less likely?

MH: To some extent the whole issue of the potential positive effects of diversity on ecosystem processes is motivated by concern about the perceived extinction crisis. There is the idea that if we can show that losing species will cause ecosystems to deteriorate, there will be a more compelling reason to conserve wild species.

In applying these ideas from theoretical ecology to the extinction crisis, it's relevant to ask the question how extinction usually occurs. What species go extinct? For example, if we're looking at randomly assembled plant communities in an experiment, we're making an assumption that if we want to look at the effects of extinction we're looking at random extinctions.

The basic question is, what types of species are most likely to go extinct? I think there are there are three patterns that could potentially occur. One is that the rare species are most likely to go extinct. They are the ones that already have small population sizes. In general, in the United States the rare species are the ones that are on the threatened and endangered species list. Often these species are rare and are ordinarily found in small areas. These are the ones that end up on the endangered species list, and most of the species we've lost have been endemic species that were naturally restricted in their range. It makes sense that rare species would be most likely to go extinct.

The second alternative would be that extinction is random and any species is equally likely to go extinct. If this were the case then the results of these diversity experiments may be relevant to the effects of extinctions on ecosystem processes. There's little evidence, I think, that extinctions are random, although there is a question as to whether massive habitat destruction that might occur in the tropics is essentially a random extinction in which all species living in a particular area are eliminated regardless of their properties. So while massive habitat destruction may technically be a random extinction, it's generally associated with such a massive disturbance that the issue of ecosystem productivity and stability becomes a moot point. The real issue there is not the loss of species but the massive habitat destruction and disruption.

I think most ecologists think that natural communities are not randomly assembled. There's strong selection by the environment...

The third possibility is that the most abundant species are most likely to go extinct, and this doesn't fit the general concepts of population biology and conservation biology which make the rational arguments that large populations are less likely to go extinct, at least as a result of random fluctuations of population size. However, if we look at past patterns of extinction, there are I think a number of disturbing examples of abundant species becoming extinct or at least becoming functionally extinct. The way this seems to operate is mainly through the epidemiology of disease, so that the species that are most likely to be affected by a disease are sufficiently abundant that disease can spread and maintain its population.

If we look back through the past century in North America, we've essentially lost several major species. Probably the most important of these was the American chestnut, which by some accounts was 25 percent of the forest biomass in the southeastern U.S. An abundant and important tree was wiped out in a fairly short period by an airborne fungus. Similarly, the American elm, which was abundant throughout most of the eastern U.S. was also wiped out in a fairly short period of time by an insect-borne disease.

In these cases we see the most abundant species being eliminated, which would lead us to expect that it would have major effects on the ecosystem. Even though we've seen forests recover from the loss of the chestnut and from the loss of the elm, there's reason to believe that the ecosystems were dramatically changed by the loss of these species. But in this case it's not really a decrease of diversity as much as it is the loss of a single important species.

So to some extent the different mechanisms of extinction can be expected to have different effects on ecosystems independent of the number of species involved. Losing one dominant species has a minimum effect on species diversity, but can

Table of Contents: *Environmental Review* Volume Six

January - December (1999)

Environmental Review

Volume Seven Number Seven
July 2000

have a huge effect on ecosystem processes, on productivity, on the food available for birds and mammals.

Likewise, the loss of a single rare species has very little effect on total species diversity and probably very little effect on ecosystem processes, simply because rare species generally represent very little biomass and have a relatively small role in nutrient cycling and other ecosystem processes. Those are the two more extreme cases.

ER: There are some serious political implications of this debate.

MH: I think all ecologists regardless of what they think about the direct effects of species diversity on ecosystem processes, are concerned about the loss of species, and in particular are concerned that whatever rationale and contributions science can make toward conservation are well supported and sound. If the ecosystem function of diversity is proposed as the primary rationale for conserving diversity and then it proves not to be a valid scientific argument, there is concern that this may weaken the overall cause of conservation.

NEXT MONTH

AQUACULTURE AND SUSTAINABILITY: Rosamond Naylor

WHY DID LOS ALAMOS BURN? Thom Alcoze

Selected Readings:

[1] Biodiversity. The Coexistence of Species on Changing Landscapes. M. A. Huston 1994 Cambridge University Press

[2] Biodiversity and Ecosystem Functioning: Maintaining Natural Life Support Processes. S. Naeem. et al. 2000 Ecological Society of America. Issues in Ecology http://esa.sdsc.edu/

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