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Sea Otters As Keystone Predators

Introduction:

Sea otters in the North Pacific were hunted to commercial extinction by the year 1900. After sea otters (and fur seals) were protected by international treaty in 1911, their populations started to recover and return to shorelines they formerly inhabited. Sea otters are called keystone predators because they exert a disproportionally large effect on the ecosystem. If sea otters are present on a rocky coast, there will be kelp beds and a variety of other animals using the habitat; if sea otters are not there to keep down the sea urchins, the kelp beds are eaten away and the habitat is greatly simplified and overrun with sea urchins.

In a related development, sea lion populations in the North Pacific have decreased substantially during the last twenty years, probably because of overfishing by people. *Orcas*, also called killer whales, used to prey on the sea lions of the Bering Sea but now that sea lions are scarce, they have switched to hunting sea otters, and sea otters are once again missing from large parts of their range.

We spoke with Professor James Estes about sea otters as keystone predators, their overall recovery and recent setbacks in the Aleutian Islands.

ER: Professor Estes, what is your training?

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JE: I took an undergraduate degree in zoology at the University of Minnesota, a masters in zoology at Washington State University, and then I did my Ph.D. in biological sciences and statistics, with an emphasis on wildlife, at the University of Arizona. Currently I'm an employee of the Biological Resources Division of the US Geological Survey. I am associated with the University of California at Santa Cruz through a cooperative agreement which provides the infrastructure within which I work. I work on campus and am deeply involved in the academic program where I teach and advise students.

ER: What is your field of research?

JE: Most of my research is focused on coastal ecosystems and the impact sea otters have on those systems. Sea otters are one of the examples of a so-called keystone species; that is, a species with disproportionally strong effects relative to its abundance, on the ecosystem. My broader interest is in keystone predators, who they are, and to what degree they are important in maintaining the integrity and function of ecosystems. I've done some work on seabirds, fishes, invertebrates, and marine plants. I've also done a little work on terrestrial carnivores, but my long-term research interest has been in the sea otter system.

I began working on sea otters in 1970. I was just out of my masters program and I happened to come into contact with Robert Paine, a professor at the University of Washington, who had recently published several influential papers on the role of sea star predators in intertidal communities. He encouraged me to think about the sea otter in that context.

Knowing what I knew about the history of exploitation and recovery of the sea otter (I was working then in the Aleutian Islands), and that history had created a disjunct geographical distribution of sea otter populations across the Aleutian Archipelago, it seemed like an outstanding opportunity for using that as a natural experiment to look at the role otters play in coastal ecosystems.

ER: Their distribution was patchy?

JE: Right. Prior to the mid-1700s, the sea otter was broadly and continuously distributed across the Pacific Rim, including all of the Aleutian Islands. The Bering expedition to the New World in 1748 discovered the Aleutian Islands and these vast fur resources, thus beginning the North Pacific maritime fur trade, which reduced otters to the brink of extinction.

When finally protected in the early 1900s, sea otters were almost extinct; only a few colonies survived here and there across the Pacific. And as the populations built back up from these remnant colonies, it created a disjunct distribution: there were places where otters were abundant, and nearby areas where they formerly were abundant but hadn't recolonized.

So it was a simple matter of looking at where sea otters were, and where they weren't but had been at one time, and then watching these ecosystems as they went through the process of recovery. That gave us a powerful tool for understanding the otter's impact on those systems.

I began working at Amchitka Island in 1970, a place where otters were abundant. In 1971 we started looking at different islands in the Aleutians. Our first glimpse at an island that lacked otters, Shemya Island about 150 miles west of Amchitka, revealed an ecosystem so startlingly dissimilar from Amchitka that the story was clear. And that story is that the otters were limiting their prey populations, which included sea urchins, which are herbivores, plant eaters. Thus, when the otters were taken out of the system, the sea urchins became abundant and mowed down the kelp forests, thus having a wide array of effects on the coastal system.

ER: Why don't sea otters spread out more? They seem to be stay at homes.

JE: One of the behavioral characters of sea otters that makes them well suited to the approach that we've taken is that they don't move around very much. Most individual sea otters don't travel more than five or ten miles of shoreline during the course of their lifetimes. That basic behavior made the recolonization of islands a fairly difficult event and that preserved many of these islands as otter-free for quite a long time. Sea otters are limited to shallow water because they have to dive to the sea floor to get food, and so they can't simply go out into the open sea and make a living by feeding on fish like most other marine mammals do, and that restricts their distribution to the near-shore environment.

The North Pacific maritime fur trade reduced otters to the brink of extinction.

They are well adapted to surviving and functioning in that zone. Their fur is their principal means of insulation. That's what keeps them warm in the cold water, and that's what made them so valuable to the fur trade. They have a well developed dentition for feeding on invertebrates with tough exoskeletons like clams and crabs and sea urchins. They are also tool-users, which further allows them ease of access to these sorts of prey in that they can break them open by using rock tools.

ER: They put the rock on their belly, don't they?

JE: They put the rock on their chest and usually beat the prey on it, or occasionally some individuals will put the prey on their chest and break it with a rock held in their forepaws. There's a lot of individual variation in the details of their feeding ecology and their feeding behavior. Some of them will specialize on urchins, others on mussels, and still others on different prey types.

ER: Are they territorial?

JE: Sea otters are territorial. They have a strongly polygynous mating system. Males maintain territories from which they actively exclude other males. Females tend to live in those territories, and so the males defend territories in which they apparently increase their reproductive success by competing for females in those areas. But there's no evidence that males influence female behavior.

So, sea otters are not highly mobile animals and they live in very high population densities, and those two characters make it possible for males to compete for females, and for

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successful males to effectively sequester large numbers of females, which are the limiting resource to their reproductive success.

ER: Wouldn't a bachelor be forced to explore new territories and wander around?

JE: They do. In fact, that is generally the vanguard of expanding populations: large groups of males that are apparently unsuccessful territory holders. The spatial ecology of the sea otter is typified by large, often very large groups of exclusively males, sometimes as many as 1,000 to 2,000 animals. That's unusual, but it's not at all unusual to see groups of 100 or more, all males.


Photo Richard Bushich

ER: Where do they get females?

JE: Well, they don't. These males are excluded from the prime habitats. It appears as though the male territories are dictated by areas that are suitable for females with pups, and so where you tend to see these large groups of males is in very exposed places, marginal habitats.

ER: Is the sea otter on the endangered species list?

JE: The California sea otter is listed under the Endangered Species Act as a threatened population. No other populations are listed as either endangered or threatened under the Endangered Species Act, or depleted under the Marine Mammal Protection Act. Those are the two pieces of federal legislation that pertain to sea otters in the U.S. The Canadians and the Russians also have regulations that protect the species.

ER: Were they endangered at one time?

JE: They've never been legally listed as endangered, only because the Endangered Species Act is much more recent than the endangered status of the sea otter. They had recovered to such an extent when the Endangered Species Act was written in 1971 that they had never been listed.

ER: Were the populations so reduced that people just quit hunting them?

JE: I think that's part of it, and part of it is that protection was afforded initially under the North Pacific Fur Seal Treaty, which was signed into law in 1911; and it provided protection for both northern fur seals and sea otters. That was an international treaty among the United States, Canada, Russia, and Japan.

ER: What happens when sea otters are removed from an ecosystem?

JE: When sea otters are present, the rocky bottom sea floors are characterized by dense assemblages of kelps and other fleshy marine plants and marine algae; and large bottom dwelling invertebrates such as sea urchins, mussels, abalones, and crabs are quite rare. But when sea otters are removed, those bottom dwelling invertebrates become much more abundant, and those that are herbivorous begin mowing down the kelp forests. Fairly quickly these systems are deforested, there are no more fleshy algae left, and there are vast numbers of sea urchins. So the two conditions, systems with and

without otters, are startlingly dissimilar. Anybody would recognize them as being different at an instant's glance.

ER: There is some unhappiness in the California abalone industry because of the recovery of the sea otters.

JE: Well, there has been. As sea otter populations have expanded, they moved into areas where their food resources had built up to high levels. In the interceding years between when sea otters were exterminated from these areas and when they recovered, large standing stocks of shellfish have built up, and people have developed livelihoods and cultural values around them. And then as the otters recovered to their more normal historical situations, they depleted these food resources and thus created a conflict with the people that have come to be dependent on them either recreationally or commercially. And it isn't just abalone. Virtually every shellfish species valued by people that live in shallow enough water for otters to get to them is a potential fisheries conflict.

ER: Adding or deleting the sea otters seems to set off a chain reaction in the ecosystem.

JE: That's right. As the sea urchins become more abundant, they remove the kelp, and that has a broad array of both physical and biological effects on the coastal system. For instance, kelp provides habitat for many species. It provides food, either directly or indirectly, for many species. It's a major source of primary production in the coastal zone, so by way of photosynthesis it provides organic carbon for the rest of the food web. It also creates drag on the water and attenuates wave and current action. *[Primary production refers to the carbon fixed by photosynthesis in plants, the base of the food web. Ed.]*

ER: It dampens the physical energy that hits the beach.

JE: That's right. So that there are all sorts of things, many of which have yet to be very well described or studied, but many processes are impacted by the presence or absence of kelp beds indirectly.

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ER: Is the kelp bed advantageous to the sea otters?

JE: It is. The kelp bed serves two beneficial functions to the otters: one is that it provides physical habitat for them in which they find some protection, and a substrate for resting. They rest in the kelp, they wrap themselves up in the surface canopy and they get away from potential predators such as sharks and killer whales.

In addition to providing habitat, the enhanced production from the kelp forest elevates the abundance of the otters. The system, which has a carrying capacity for otters that is determined by the level of plant production, is essentially kelp-free when sea otters move into it; by enhancing the kelp beds, that carrying capacity is elevated, which in turn elevates the local population of sea otters. So by reducing the herbivores, primarily the sea urchins, they are stimulating the kelps, which has a positive effect on the otters, which in turn creates an even stronger depleting effect on herbivores. It's a positive feedback system.

ER: Kelps and sea urchins co-exist all around the world. Why are the North Pacific kelps so vulnerable to grazing?

JE: It appears that over the millennia, the strongly limiting influence that otters have on herbivores has created an environment in which there has been virtually no selection in the algal populations for defense against grazing. And so the plants have evolved no defenses against herbivory, and as such they are extremely vulnerable to intense herbivory.

It is now well known that many marine algae use chemical defenses to protect themselves against their enemies, the herbivores. If we go to a part of the world where kelp forests have evolved in the absence of otters, we find plants that are very well defended chemically; they produce secondary metabolites that are toxic or

noxious or a deterrent to herbivores. Pacific kelps typically have very low levels of these secondary metabolites, and that's probably why the system has reacted so strongly to the removal of otters and the increased abundance of plant-eating organisms.

ER: What effect do killer whales have on sea otters?

JE: This is something we just published in *Science*[1]. The story is one that we have put together through the 1990s, taking a long-term view of the Aleutian Islands again. Beginning in the early 1990s, *orcas* began eating otters; and they've driven the otter populations to quite low levels again over large areas of the Aleutians. And as a result those systems have since shifted back to being herbivore-dominated.

Previously the *orcas* were probably specializing on seals and sea lions, and with the collapse of the Bering Sea ecosystem and the decline of seals and sea lions, we believe that the whales have shifted their diets to include otters. The otters are extremely vulnerable to orca predation and there were relatively few of them compared with the historical seal and sea lion populations, and thus the *orcas* apparently were able to drive the otter populations very rapidly downward. These declines have been in the order of about 25 percent a year, which is a catastrophic decline rate. We have seen this over thousands of kilometers of habitat in the Aleutian Archipelago.

ER: Are you sure it's due to *orca* predation?

JE: We've observed *orcas* eating sea otters, and we've done a lot of subsequent analyses to look at all of the possible explanations, and everything pretty much falls into line with *orca* predation. It appears as though the cause of this sea otter decline is rooted in the open sea, but the *orcas* have formed the linkage between the disturbance in the open sea and the radical changes that have occurred in the kelp system as a consequence. We've done some energetic analyses on this based on the caloric value of otters and the needs of *orcas*, and it turns out that the population declines of otters that we have observed could have been caused by just one group of three or four *orcas.* It may be that one group discovered otters and have been making a living on them and going from island to island. I'm convinced now that it's the *orcas* that caused the sea otter populations in the Aleutian Islands to crash.

There's always some uncertainty, but all the evidence we have points to it. For one, there has been a complete absence of any dead otter bodies, which is very peculiar because when otters die, they tend to show up as beach-cast carcasses. And if starvation, or disease, or a major pollution event like the Exxon Valdez spill were the cause, whenever otters die from those reasons, you find large numbers of them on the shore. We found nothing, so that's very suspicious. And there are other sources of evidence that points to *orca* predation as well.

ER: Are sea otters a special case, or is it normal for predators to influence their habitat so much?

JE: That's a good question. Is this an unusual situation, or do apex predators typically control ecosystem function? It's still something of an open question, but there are a number of other case studies of high trophic level carnivorous mammals that are beginning to surface that are causing us to believe that it is a more general phenomenon in nature.

ER: Aldo Leopold observed that the absence of wolves led to a population explosion of deer. Was that just anecdotal evidence?

JE: Most of those experiences were anecdotal; our work is anecdotal. It's the kind of a problem that is hard to put to a direct experimental test. I think the nature of the evidence in the sea otter case is much stronger because of being able to observe their influences in different places. That is almost as good as a planned experiment.

Many people have long thought that the loss of terrestrial carnivores, for instance in North America, had a big impact on herbivore populations and subsequently on plants. So there is nothing really new about the idea, but the evidence is beginning to accumulate. The problem with the wolf/deer story is that it's anecdotal on the one

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hand and confounded by other explanations on the other. But there are a number of other case studies now. For instance, there was an interesting study published in the early 1990s about Isle Royale looking at the dynamics of wolves, moose, and balsam fir, and there the story was very similar to our otter story. The conclusion was that wolves had a big impact on the moose and consequently on the structure of the plant community. *[Brian McLaren described his Isle Royale fieldwork and results in the April 1995 issue of Environmental Review. Ed.]*


Photo Graeme Ellis

And there's ongoing work in the New World tropics by John Terborg and his colleagues where they're using newly created islands formed by impounding rivers to look at the dynamics of the terrestrial ecosystems in these islands. In essence, the hilltops that protrude beyond the surface of these newly formed lakes are now islands in what earlier was an unbroken tropical forest. These island habitats are so small that the carnivores have been lost, in this case it's mostly jaguars and pumas and harpy eagles. And what Terborg is seeing on these fragmented island habitats is very similar to what we've seen in the Aleutians; that is, an explosion of plant eaters, and the collapse of the plant assemblages as a result of it.

There are numerous other examples that don't involve carnivorous mammals. Bob Paine's work, for instance, on *Pisaster* [a predatory sea star] is one case. The lake work that has been done by Steve Carpenter and Jim Kitchell at the University of Wisconsin is probably the most well known, but there have been a number of people that have done whole-lake manipulations where they have removed top-level predators, mainly fish like bass, and found a cascade of effects through the food chains eventually going down to the plant populations.

I'm interested in the question of the generality of this process and the extent to which carnivores may be important from a conservation perspective in maintaining the integrity of ecosystems.

ER: How could they not be important?

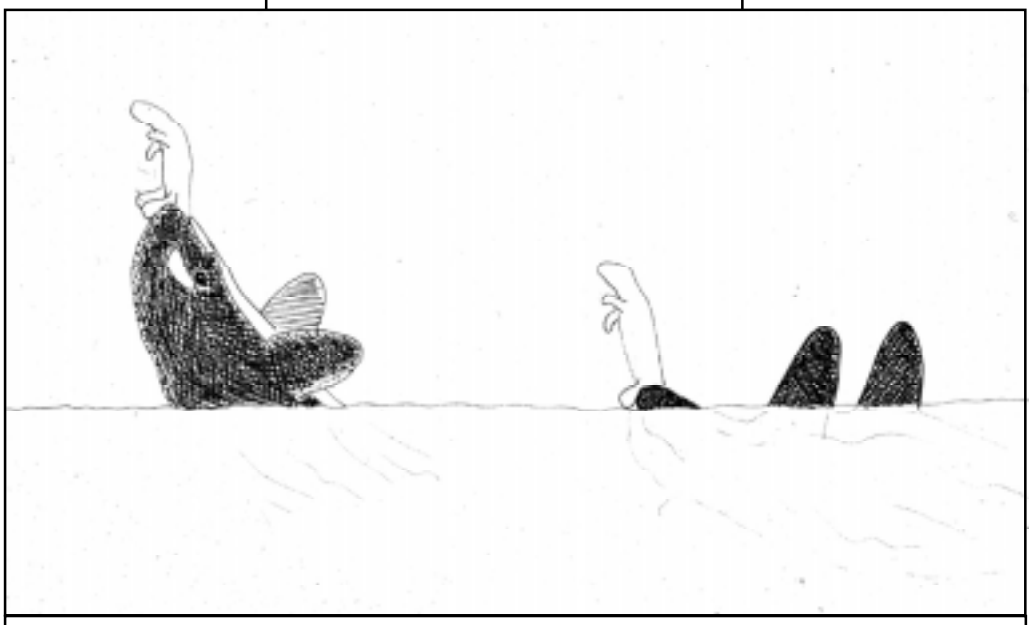
JE: A dichotomy of views has emerged: the early view, still embraced by many is that top-level carnivores do no more than serve as the receptacles of carbon, energy, and nutrients flowing upward through food webs, and by the time these materials get that far up, it's not terribly important. This is the bottom-up view of ecosystem function. And thus whether top predators are there or not may be important esthetically, but functionally it is of little consequence.

The alternative top-down view holds that the predators play a more dramatic role in ecosystem function. There is growing evidence for this view in many systems. And thus the importance of top predators to the maintenance of these systems from a

conservation and management perspective may be much greater than people have acknowledged or recognized in the past.

ER: Well, that was Aldo Leopold's insight, wasn't it?

JE: Yes, not surprisingly. He had many, he was way ahead of his time. And I think he had the perspective of nature to suspect these things and to see bits and pieces of evidence. But the evidence now, a half a century after Leopold, is in fact confirming the importance of predators in more detail than he could have imagined.



This artist's rendition of the only known photo of a killer whale attacking a sea otter portrays the attack in two stages: on the left, as the photographer first saw it, and on the right, as it appears in the photograph taken moments later after the whale had fallen back into the water with the otter in its mouth.

Photo Scott Anderson - Drawing Greg Meyer

ER: You mentioned in passing the collapse of the Bering Sea ecosystem. Are humans the top predator there?

JE: Humans are top predators almost everywhere. But the role humans have played in the Bering Sea is a controversial point. The collapse of the system, may be not quite the right word, although it's a term that's been used a lot. But recently there have been drastic changes in the Bering Sea ecosystem. In particular, there have been clear changes in many of the top-level consumers, mostly animals that eat fishes. Populations of sea lions, harbor seals, and a variety of fish-eating seabirds have declined, in some cases catastrophically. Stellar sea lion populations in particular, have declined tremendously in the last two or three decades. Many people suspect that the ground fishery of the Bering Sea has played a significant role in these declines. However, it's one of those problems that is so vast and difficult that it's been hard to make a compelling strong argument, and to obtain strong evidence, other than that we are taking tremendous quantities of fish from the Bering Sea ecosystem. And so I think many people either believe or strongly suspect that the activities of humans through exploitation of the fishery is the major driver.

People have also speculated that the removal of the great whales from the North Pacific ecosystem has perturbed the food web. In this case the proposed scenario is that removal of these plankton-eating whales has allowed the zooplankton populations to increase. *[Zooplankton are tiny animals that make a living eating microscopic floating plants (phytoplankton) Ed.]* Pollack, which also eat zooplankton, have thus responded by building up tremendous standing stocks that in turn, either through predation or competition, have caused the other fish species to decline. Pollack probably are more abundant now than they've ever been in the Bering Sea, but many other fish species are less abundant. Some people think those other species of fishes were crucial in supporting abundant sea lion populations. Pollock have less fat than other fishes and don't provide enough energy to maintain the sea lions.

I'm not enough of an expert on that system or those issues to have strongly held views on exactly what has happened. I do know that the Bering Sea ground fishery is one of the most intensive in the world in terms of landings. And it's also very clear that most ocean fisheries have substantially reduced standing stocks

of fishes, in turn having related effects on other parts of the ecosystem, so it shouldn't surprise anyone that the pollack fishery would have perturbed the Bering Sea ecosystem, given how intensive it is.

You're always going to have the naysayers because the evidence is far from airtight, and there are major economic interests involved. So in the absence of a compelling analysis that can exclude other possibilities, the argument that fisheries caused the sea lion collapse is controversial. But I'm not sure how controversial it is among people that don't have a vested interest; that is, oceanographers and ocean ecologists. I think these folk generally feel that fisheries have substantially effected the Bering Sea ecosystem.

What Value Remains in A Cut-Over Tropical Forest?

Introduction:

Most tropical forests have been logged or will be in the near future. While a forest in a temperate part of the world will have a dozen different kinds of trees, an equivalent area of tropical forest will have several hundred different species of trees. The same is true of bird species, plants, insects, fungi: all forms of life are more diverse in the tropics than in temperate regions. This is one reason why conservationists are so concerned about tropical forest losses. Logging a tropical forest not only takes out the trees but the habitat for a multitude of different species. Managers, governments, and conservationists are making decisions about how to use and/or conserve tropical forests when very little is known about what kind of trees and other life forms are in them, or how they all work together to form ecosystems.

In Indonesian Borneo, Chuck Cannon studied the forest diversity that remained after a mahogany-dominated forest was logged. He and his coworkers were surprised to find that selectively cut forests had a diversity of tree species similar to unlogged forest. This should not give comfort to those who want to log tropical forests, rather it points out that much of their biological value remains, even after their commercial value has been extracted; that is, logged over forests could be valuable as buffers and corridors for existing parks and conservation areas. We spoke with Chuck about his work in Indonesia and its implications for tropical forest management and conservation efforts.

> We saw that the small trees in the remnant stand were still quite species rich, even in comparison to unlogged areas nearby...

ER: Chuck how long have you been working in Indonesia?

CC: I originally went to Indonesia in 1987 as a research assistant to Mark Leighton when I was an undergraduate at Harvard. I was a biological anthropology student interested in primate behavior. I spent a year as his research assistant at a research site in Gunung Palung National Park when he went there to set up a broad-scale ecological research station. My responsibilities were not just studying primate behavior, but also vegetation surveys and looking at the patterns in the forest. I spent a year there then and continue to go back.

After I finished my undergraduate education I got into some conservation jobs: a training course for Southeast Asian scientists based at that research site. Then I got a job with Wildlife Conservation International and went to Cameroon, West Africa for about six months as a field biologist doing a biological inventory in a national park. Then I and Deborah Lawrence, who is now at Harvard Forest as a post doctoral fellow, got funding to go to Indonesia and study Gunung Palung National Park. The park is surrounded by logging concessions, and we wanted to know what types of forests were surrounding the

park. There was very little information about what was happening to selectively logged forests worldwide, even though it is such a big issue in the media. So we gathered baseline data to get an idea of the condition of the forest after selective logging.

We spent a year and a half there in 1991-92. My co-authors and I set out to describe the structure and the species composition of a selectively logged forest. We selected a mid-sized logging concession outside of any kind of major government management program. The logging companies follow the silvicultural guidelines put out by the Indonesian government, but there is very little presence of government there. Overall, in that context, it appeared to be a fairly typical logging operation in Indonesia.

Our first paper describing the basic structure and forest composition of this area was published in 1994[1]. And I then joined the graduate program in botany here at Duke and started out on a different trajectory studying systematics, and this data was put on the back burner for a while.

ER: What is your academic training?

CC: I am finishing my Ph.D. in systematics in the botany department at Duke University. I have been studying the evolution of tropical oaks and their reproductive biology in mixed communities. I was disenchanted about the future of the forests in general and so I wanted to go into more pure science. I am becoming more positive again about their fate after realizing that these forests do not disintegrate with the first touch. Other scientists have been seeing the same kinds of patterns in different forests worldwide, like Ed Webb in the Costa Rican swamp forests and Guaraguiata in Brazil after clear-cutting and grazing. I think this kind of research is going to be important in the near future because the sad fact of the matter is these forests are quickly becoming all that we have to work with in order to save biodiversity.

ER: What did you find in the logged-over area?

CC: We saw that the small trees in the remnant stand were still quite species rich, even in comparison to unlogged areas nearby, and I was quite surprised by the result. It was a little troubling because I did not know how to interpret it. It was against what a lot of people were saying and I was not exactly sure how it would be received.

> If these logged-over forests are not valued and incorporated into wider conservation schemes, we are losing the chance for capturing a lot of degraded land that no one really values very highly economically.

So I put it aside and wrote a much longer manuscript discussing the overall change in floristic composition in the area. But with my coauthors, we decided to pull that single point out of the longer manuscript and let it stand on its own. We felt it was compelling enough.

ER: Was the park your control area for the logged over forest?

CC: No, the park was not the control. It was the point of reference and is the center of our long term studies. The park has a mountain range running down the center of it, and the area to the north where we worked is more undulating hills with swamp mixed in. The forest habitats change very quickly from flooded swamp forests to lowland hill forests.

In doing the initial surveys I spent a lot of time talking to the head surveyor of the logging company to figure out when it had been logged and how it had been logged. And that history was fairly complex because even though we had a nice little map that we received from the government offices showing in blocks the logging history, when you take this to the head surveyor and put him on the back of a motorcycle and drive him around, things are very different than what it says on the map. There are reasons for that: the logging company receives the concessions from the government and these blocks are drawn on the map in big arbitrary rectangles without any knowledge of what's in the rectangles. So the logging company is forced to do what will work and ignore the plans that are on the paper because they don't refer to anything sensible.

We wanted to choose an area that had been logged at some definite time in the past, hopefully more than a decade, and we wanted to compare it with a recently logged forest and to see if we could detect any changes between the two. Originally we were thinking that the control would be inside the park where no logging had occurred before, but in our initial

surveys we realized that there were patches of forest in the concession that had not been logged because they were isolated little hills anywhere from one to not quite ten hectares, little islands of hill forest surrounded by swamp forest. *[One hectare is about 2.5 acres. Ed.]* And that is what we decided to use as a control.

We were fortunate that we'd found these local controls because the dominant tree species in the forest were completely different than the dominant species in the park just sixty kilometers south. And in fact one of the dominant species that they were harvesting isn't even present in the park.

ER: These were tropical hardwoods?

CC: Yes, they are all in the family *Dipterocarpacaea*, commonly called Philippine mahogany. They use it for plywood mainly because it peels very nicely. It's also the dominant group of plants in those forests, and so they target those trees; they were mainly taking out just three mahogany species.

We finally chose an area that had been logged eight years before, and two smaller areas, one had been logged one year before and the other had been logged just six months previously. We wanted to look at the basic structure in these three study areas.

ER: What do you mean by structure?

CC: When I say structure, I mean the tree canopy that is present, whether or not there are large open areas and isolated trees standing by themselves, or whether the trees are largely connected in some fragmented way. If the holes in the canopy created by the logging are fairly small, the canopy would still be fairly intact and connected. I think that the apparent damage just becomes overwhelming as you travel along the roads and walk the skid trails because you are constantly confronted with this moonscape of orange compacted soil, but if you walk straight through the forest, there is a surprising amount of canopy remaining.

And so we wanted to know simply how large were the gaps that were created in the canopy and what was the change over time. Were the gaps small and close together, creating a patchy tree canopy that had lots of little holes in it? Or was it one big area that was basically empty of trees and then strips of trees on the edges? We created a classification system for that: whether or not the canopy was totally open; whether or not there were isolated trees standing around; whether or not there was a tree canopy that was basically closed but was still rather fragmented with some trees missing from the canopy; or whether or not the canopy was basically like an unlogged forest. To do that, I walked along a transect and kept track of what type of forest I was in.

We discovered that about half the forest was heavily disturbed, it was either completely an open canopy or isolated trees, but fully 15 percent of this forest had escaped logging entirely. After having assessed the landscape structure of the forest, we wanted to measure the density of the trees. How many trees are there? How many stems per hectare? And so we randomly selected a few locations inside the study areas and looked at what kind of forest remained in that plot. We measured the diameter of all the trees in these plots and then collected leaf samples to identify them. We looked at the species composition and from these plots estimated the species diversity of the entire area.

ER: By diversity you mean just the plants?

CC: Just the large trees. We didn't do any animal surveys. We were interested in the remnant stand of the forest. We felt that the major changes that were going to happen in this community were going to be influenced by what trees were still standing.

ER: Why not pay attention to seedling establishment?

CC: There has been some previous work on seedling establishment in these areas, and it looks pretty bleak. Cut-over forest is a very different environment than most seedlings germinate into in a closed canopy, unlogged rainforest: the humidity is much lower, the heat is much higher, the ground is oftentimes compacted or eroded.

We felt that the trees that were going to grow into the canopy would be the poles and the saplings that were

Immediately after logging, the stem density of the entire forest is reduced by half, and there is a lot of damage done to the trees that are left behind.

already there. They would be able to respond much more quickly than seedlings would. Many tropical trees spend a long time at a small size, four or five centimeters or maybe ten centimeters in diameter. They'll spend decades at that size waiting for a chance to grow into the canopy. They are shadowed by the trees standing above them and they're waiting for the canopy to open up so that they can then grow up into their mature position in the canopy. And so we felt that those trees, that were of juvenile status, would be the ones that would grow into the canopy and would have the most influence on the regeneration of these areas. We only measured trees down to twenty centimeters diameter at breast height (DBH), about eight inches in diameter.

ER: What was the number of species you had to deal with?

CC: In the park we have found 600 species of tree in only seven hectares of forest, but this includes a wide diversity of forest habitats and soils too. The levels of dominance of any one species are very low as well. When I say a tree is dominant, I mean that it might make up 5 percent of the stand. Even the dipterocarps as a family rarely ever achieve more than 25 percent of the stand.

ER: How many trees were taken out by logging?

CC: About eight trees per hectare, but these trees are large, usually over a meter in diameter. Most of the disturbance that occurs in selective logging is the caterpillars driving around to drag the trees out, the creation of roads and landings where they pile up the logs to load onto trucks.

I was asked by one person why the logging levels are so low in these forests, and I think it is simply because of the inherent high diversity. These logging companies are not doing this out of the goodness of their heart. They want to harvest as much quality timber as they can, but if they harvest twenty different kinds of timber, they have to find twenty different people to sell it to because the sawmills are prepared to deal with only certain kinds of wood. So in some ways I think the diversity of these forests has helped to protect them.

The level of harvest is fairly low, even though the amount of damage is still quite high. Immediately after logging, the stem density of the entire forest is reduced by half, and there is a lot of damage done to the trees that are

left behind. The forest density doesn't recover very quickly. Even in the forest eight years after logging, the density of all the trees was still roughly half of what it was in the unlogged areas.

ER: Have the canopies grown back?

CC: In some areas it was more closed but there was not overwhelming closure. In the really open areas where trucks had been driving and where the caterpillars went, the soil was very compacted, some of those areas were not closed and the species were all invasive pioneers. But there was some closure. The open gaps were getting smaller and the amount of fragmented canopy was increasing in this eight-year forest, even though the density of trees had not recovered that much.

ER: Would you expect the density to recover rapidly?

CC: Almost all the trees in this study were already in that forest before the logging, and so if there's a reduction in the density of trees, they should basically stay at that density until a new recruit class grows in. And trees are now growing at different rates. Some trees will grow more rapidly than they would in an unlogged forest. That's been the ideal of the silvicultural systems or these sustainable logging systems; that is, when you cut down the forest, you're releasing the trees that are left behind and they're going to grow more rapidly than they would in unlogged forests. That way you're supposed to get an increase in timber volume at a much higher rate than you would see in unlogged forest. That's been the hope and dream of tropical foresters.

ER: It seems like trying to get something for nothing.

CC: Right, and it's also based on no information. The population biology of the vast majority of these species is not understood in the least, from seedling germination to their reproductive biology and everything in between. All the regulations and rules have been created in a vacuum.

First of all, we didn't find this increased growth that the loggers were hoping occurred. We didn't see a vast number of trees growing into the size classes that could be harvested in the coming decades. There was almost none. Very few of the trees had attained fifty centimeters DBH in that eight years. That indicates that this increased growth in the remaining trees in the forest is going to occur much more slowly than anticipated, if at all.

But the diversity in the smaller size class of trees seemed to match the diversity in the unlogged forest, and this without an increase in density. This says to me that the dynamics of the forest in recovery are different than in unlogged forests, the dominance in the recovering forest is much lower.

It seems like there has been some positive response by the trees that have been waiting for a more open canopy and more light. There have been some taxonomic composition changes, but overall, there is no great shift towards pioneer species; there is no one dominant species that is taking over.

Most of the pioneer species in these forests are fairly short lived, they grow to maturity in a decade and they flower for ten or fifteen years and then they die. So the turnover rate for that initial class of pioneer trees is pretty quick. We're looking at the rainforest trees that would probably comprise a mature canopy; it's only that we're seeing a much more even regeneration of the trees.

To me this points out that these forests are still valuable for conservation of biodiversity, for potential non-timber forest products, or perhaps even timber.

And also it points out that the conversion of these forests into plantation forestry, particularly oil palms, is where a major loss in biodiversity is occurring. If these logged-over forests are not valued and incorporated into wider conservation schemes, we are losing the chance for capturing a lot of degraded land that no one really values very highly economically. We can capture that biological or conservation value at relatively low cost into broad conservation schemes.

In this example conservation areas that surround a national park can be used as buffer zones. If we keep them as logged-over forests and let them regenerate naturally they can perhaps

provide corridors for animals, for birds, primates, so that they can move between protected areas. For instance, to the north of this concession we studied, there are a few isolated little mountains that have not been logged and are protected by the government.

ER: How long do you think it will take for this logged over area to recover?

CC: We don't think the forests are going to regenerate back to the pristine state, that's not the expectation. There have certainly been drastic changes, and there are many things that we didn't measure. The seedling establishment may be quite low, as it has been seen in other experimental studies, so we may be missing a generation of trees. But if these canopies can close to a certain degree and they can be kept from all the other potential things that can happen, for instance, forest fires that we've seen recently in Borneo, the recovering forests could be quite valuable. A Dutch Ph.D. student, Martjan Lammertink, who is studying the effects of selective logging on woodpeckers and wood-boring invertebrates wrote to me recently via email. He said that he had to abandon his research sites in East Kalimantan because of the vast fires there last year. Almost 150 by 300 kilometers, more than 4 million hectares, of pristine and disturbed forest burned, including some very unusual habitat types. A lot of that has to with selective logging. Forests dry out much more quickly than they do when they are not logged, so they are more vulnerable to fire.

ER: Is logging the main threat to these forests?

CC: There are issues of land tenure. The local villagers don't have legal ownership of many of the lands they consider traditionally as a part of the village. So they are doing things like clearing land just so they can plant rubber plantations that they don't need or they don't have enough manpower to harvest, mainly just to claim ownership for these areas, and so the rates of conversion of these forests is rapidly increasing.

Although it might not seem like it, governments and international lending agencies are listening to our debate and if we sit here as biologists and say that secondary forests are worthless, they are going to believe us and allow it all to be converted into other land uses, much more intensive land uses, like plantation forestry. In that situation, you will have small areas of core old growth reserves surrounded by a biological desert of oil palm and rubber trees. I don't want that to happen. I think there have been many missed opportunities there, but this is one that we wanted to highlight: that these forests are still quite diverse, they have the potential to become quite diverse, and should be incorporated into wider conservation schemes.

> The population biology of the vast majority of these species is not understood in the least, from seedling germination to their reproductive biology, and evertything in between. All the regulations and rules have been created in a vacuum.

ER: I sense that you were concerned about having your research misconstrued by people who want an excuse to cut more in the forests.

CC: Yes, that's one of the reasons it's been so long for this research to be published, we were debating about how exactly to present it or how to interpret it, and also all the possible misinterpretations. We didn't want to be seen as giving the loggers the green light. But we felt that this finding was important enough, and the speed with which things are changing in this area, economically, the fires, we felt we needed to publish this information and bring some attention to these logged-over areas.

The sad fact of the matter is that a vast amount of tropical lowland forest already has or probably will be logged worldwide and there's not much that we can do to stop that. Much of the logging is occurring without any kind of government enforcement. The silvicultural regulations are basically just on the books and they are not really followed by anyone. There are a few exemplary logging companies out there in Indonesia and pilot studies have been done of their operations and different kinds of experimental forestry. And yet I doubt anyone's ability to implement these measures on a large scale.

Reduced-impact logging and different methods of sustainable forestry have all been done in small areas, but look at the condition of the Indonesian government right now. They're not going to be able to enforce strict requirements about replanting or even about harvesting a particular area. They don't even have

adequate inventories of what's in the forests before they go in and log, so knowing what the logging company did is very hard to know after the fact.

Developing more efficient, less damaging, more sustainable silvicultural systems is important, but a lot of the logging has already occurred and a lot of it is going to happen outside of the government realm of influence. Knowing what's going on in those forests is important, and we hope to continue to follow this forest. People seem to be realizing that selective logging does not equal deforestation, and we need to be more rational about these decisions and look more carefully at what's happening in these forests.

The fact that these forests aren't clearcut to me is heartening in itself. I spent most of my time in Malaysia last year and there's been a decline in logging activity in remote areas of Sarawak on the island of Borneo. The prices are dropping off; importing logging equipment is prohibitively expensive now. And in some ways these areas may be protected by their remoteness. But then the drought facilitated conversion of those areas into plantations. So the trajectory of these forests is difficult to predict, not only because of the biology, but because of the larger political and economic context.

ER: It seems like this is just a temporary economic downturn and in ten years we'll be back at it.

CC: So in some ways to me it's maybe an opportunity to capture some of these logged-over areas into conservation schemes, if we can get the government to commit. They do enforce some regulations if it is brought to their attention.

ER: Would it be fair to characterize your work as showing that these cut over forests have value where none was seen before?

CC: Yes, that's pretty accurate.

ER: How can that insight be implemented in creating buffers and enlarging protected areas?

CC: I think the opportunity cost for these areas is still pretty low. Our research shows the timber volume is not increasing rapidly and the recovery as valuable timber harvest is still far in the future. So these areas are almost valueless in a straight-ahead economic sense. But I think that one of the first things that could be done is to target these logged-over areas that surround parks that might provide corridors between protected areas, to highlight those areas and recognize them as being valuable and say, OK plantation forestry is good within reason, but let's not put plantations here. And you can put your plantations in this area, that's next to the urban areas which may have less conservation value because of its position.

If we can make a strategy based on the logged-over areas' position in relation to unlogged areas or areas of particularly high biodiversity, that might be the first step. And then also recognizing that the villagers that live in these areas still have their rights to this forest. They extract a much more diverse type of product from the

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forest. Perhaps giving them extraction rights to these areas for other kinds of timber, high quality tropical timber that can be used in furniture making or rattan products or other kinds of products that might be used more locally, emphasizing that type of a value in these areas might enhance their chances of surviving.

Also I think there's a lot of room for research on the changing dynamics of these forests. We've shown that there's a high tree diversity remaining in these forests, but there are many other interactions going on. The primate community has moved away; you don't see nearly the density of primates in cut over forests that you do in the protected part. Are they going to come back like they have in some areas, or are these populations going to remain depressed? There are many different interactions that are going on. Dipterocarps need to have fungi associated with their roots. Are those fungi going to be able to survive in this changed environment?

ER: That soil ecology may play out over many decades.

NEXT MONTH

HUMAN HEALTH IIMPLICATIONS OF LEAD IN THE ENVIRONMENT: BRUCE LANPHEAR

LARGE CARNIVORES NEED BIG PROTECTED AREAS: GINSBERG & WOODROFFE

CC: Right. The eventual outcome of this disturbance is yet to be seen, by a long shot.

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