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CHAPTER FIVE

The Long View: Old-Growth Rain Forest Food Webs

This chapter is about ecological richness and relatively unexplored terrain filled with possibilities. Considerable trophic cascades research has been done in tropical forests, as in the Amazon, but little has occurred in the Pacific Northwest region of the United States and Canada, which contains ancient temperate rain forests, termed *old growth*. Here we will examine some of the studies from the tropics and then look at Pacific Northwest old growth, including its physical characteristics, our increasing awareness of this forest type's ecological relevance, and potential trophic cascades. We will see how trophic cascades may be occurring at two leading experimental forests: the H. J. Andrews in Oregon and the Wind River in Washington. On the basis of well-documented trophic cascades in other types of ecosystems, we will examine how temperate old-growth forests offer further opportunities to learn about these interactions.

Rain forests occur in the tropics, near the equator, and much farther north, in the Pacific Northwest, as well as in other places, such as Tasmania. Invaluable to our planet's health, rain forests convert large amounts of carbon dioxide into oxygen and provide homes for an astonishing diversity of life. Defined as thick evergreen forests that receive at least eighty inches of rain per year, they cover 7 percent of the earth's land surface and contain as much as 50 percent of known species.[1] They are diminishing rapidly as a result of agricultural conversion and other forms of human land development.

Ecologists characterize old growth, also known as *virgin* or *legacy* forests, as stands more than 200 years old that contain great structural variation. If you take a walk in old growth you will discover trees of all ages, from young to very old; a canopy with multiple levels as you look up into it; standing dead trees (called *snags*); openings made by fallen trees and fires; and abundant dead wood. Openings in the canopy allow light to reach the soil, enabling shrubs and young trees to grow, adding to this system's structural richness. This physical complexity harbors a highly diverse community of plants and animals.[2]

Forests are arranged in layers, ranging from the upper canopy to the soil, each providing distinct habitat. Any mature forest has five horizontal layers, plus one that defines riparian zones. The *canopy*, which has three layers, comprises all foliage, twigs, and fine branches and their flora, fauna, and interstices (the air between them). The *upper canopy* contains the tops of older trees and in coniferous forests the *cone zone*, the area of primary cone production. The *mid-canopy* contains the middle foliage, and the *lower canopy* consists of bottom foliage and sapling tops. Immediately below the canopy lies the *understory*, defined as the area between the ground and the base of the tree foliage, typically filled with shrubs, mosses, and herbaceous species such as wildflowers. The soil forms the base layer, made up of inorganic material and plant roots and inhabited by insects, small mammals, and mycorrhizal fungi, which have symbiotic relationships with tree roots. Finally, the *hyporheic zone* makes up the below-ground hydrologic system fed by stream water. It provides a spongelike interface between terrestrial and aquatic regions where nutrient exchange takes place.[3]

Ecologists Gary Polis and Donald Strong refer to trophic cascades in systems with high biodiversity as "trophic trickles" because food web complexity across a spectrum of multiple herbivores, carnivores, and detritivores (species that obtain nutrients by consuming decomposing matter) creates many pathways for energy movement. We saw in chapter 3 how coral reefs provide examples of this. Old-growth rain forests, whose diverse structure encompasses whole watersheds, provide another example. Accordingly, we'll look at food webs at various levels in these forests, from the top of the canopy to inside the soil.

The Empty Forest

In the 1990s conservation biologists Kent Redford and John Terborgh identified a phenomenon called the *empty forest* whereby apparently rich tropical forests lacking keystone and other animal species undergo changes in plant communities. These effects move through a food web, influencing everything from tree growth to soil function to wildlife habitat, and can be as damaging as deforestation. Plant community changes occur anywhere large mammal populations have been overharvested by humans or reduced or eliminated by climate variability. These effects can have long-term influence; indeed, many forests reflect events that happened thousands of years ago.

If you walk through a Costa Rican rain forest you will see hundreds of large fruits lying on the ground rotting, their seeds failing to germinate. Scientists puzzled over this mystery for years. The forest palm *Scheelea rostrata* grows in lowland rain forests from Brazil to Costa Rica and produces yellow, egg-sized fruits with thick-hulled seeds. Because many things in nature have evolved to ensure survival of species, it made no sense that this tree had developed seeds that could not germinate. In a seminal 1982 *Science* article, "Neotropical Anachronisms: The Fruits the Gomphotheres Ate," evolutionary ecologists Daniel Janzen and Paul Martin looked at this puzzle through the lens of evolutionary time. They began by considering that all species in an ecosystem coevolve, developing traits that serve specialized functions.

The food web in this landscape once contained gomphotheres, mastodon-like Pleistocene herbivores, which ate the fruits of the large, relatively long-lived forest palms. Gomphotheres ingested these fruits and moved on, probably traveling far each day. During the slow digestion process they excreted the seeds far from the trees where the fruits originated. The gomphotheres' movement patterns distributed the seeds broadly, and enzymes to which the seeds were exposed during digestion enabled them to sprout. Gomphotheres became extinct about 10,000 years ago, possibly as a result of overhunting by humans. In their absence there has been no other large mammal capable of ingesting and dispersing forest palm seeds. Janzen and Martin's megafaunal extinction hypothesis, in which they postulated that these seeds coevolved tightly linked to gomphothere feeding habits, helped solve this mystery. They further suggested that many similar evolutionary trophic relationships may have been lost because of extinction, possibly creating forests that today are different from those that would have existed had these species not become extinct. With megafauna to disperse their seeds, these forests originally may have been more dense, with a broader distribution.

Janzen and Martin's paper invited scientists to look at trophic relationships on longer time horizons. It had a profound effect on marine ecologist James Estes, inspiring his research on the plant defense compounds kelp forests produce in the Southern Hemisphere, where there are no sea otters (*Enhydra lutris*) to keep herbivores in check.[4] When I read their paper I realized that the patterns and processes I had been observing in nature had far deeper origins than I had imagined. And had I read it before I traveled to the Amazon, I would have experienced that system differently.

The Amazon Basin encompasses 3 million square miles and nine countries and has the highest biodiversity of any region in the world. I visited the Peruvian portion in the mid-1980s, traveling downriver from Iquitos in a dugout canoe and going deep into the rain forest. Since then urban growth has caused deforestation via cutting and burning, but I had the good fortune to see this area before it was logged. My first impression was of unparalleled sensory richness and the sharp contrast of the benign and the deadly—pink river dolphins (*Inia geoffrensis*) swimming boisterously next to our canoe, and cayman alligators (*Caiman crocodilus*) gliding silently toward us, their olive bodies and rugose snouts camouflaged against the muddy water.

I spent halcyon days at a primitive field camp, eating exotic fruit and feeling euphoric from breathing the moist, superoxygenated rain forest air. Not long after I arrived a man from the Yagua Tribe, who stood four and a half feet tall, carried a blowgun, and wore little more than a loincloth, led me into the forest. My barefoot guide started on a narrow, overgrown trail, gracefully pushing aside tangled vegetation and palm fronds as he penetrated the forest. We were soon enveloped in verdure, and the dim sunlight that filtered down from the canopy far above created a primeval atmosphere. Ancient trees soared skyward, taller than the nave of any cathedral, and held wonders beneath their interlaced canopy: enormous spiderwebs; boa constrictors (*Epicrates cenchria*) draped on low-lying tree limbs, their rust-and-black bodies barely visible in the half-light; and toucans (*Ramphastos toco*) streaking by, their yellow bills and breast feathers bright against the soft green foliage. The primal cries of howler monkeys (*Alouatta* spp.) provided a rousing accompaniment for our walk.

The hardwood trees and forest plants looked unlike any in the Northern Hemisphere. The massive buttress roots of mahogany (*Swietenia macrophylla*), which Peruvians call *caoba*, supported thick, towering boles, and Brazil nut trees (*Bertholletia excelsa*), the largest of the Amazon rain forest species, rose unbranched for half of their 150 feet of height. Vines called lianas coiled around tree trunks and hung from high branches, creating pathways for wildlife. Gardens of epiphytes (plants that do not need to grow on the ground) sprouted from stout limbs, some of them orchids, others bromeliads, many in bloom, their heady, sweet scent permeating the air. They had evolved mechanisms to make the most of this environment, collecting moisture and soil in their exposed, tangled root masses and cupped leaves.

I was not an ecologist back then, so I missed much, especially the signs of damage in this forest, even amid all the lush beauty. Back then I believed forests could be destroyed only by chain saws and the slash-and-burn swidden agriculture prevalent in South America. I didn't realize that large predators, such as the jaguar (*Panthera onca*) and puma (*Puma concolor*), were most likely gone from this place and that their departure had already caused great changes. In the years after my Amazon sojourn, through the writings of Janzen, Martin, and Redford, I became aware that damage to tropical rain forests can occur from within, less visibly and more insidiously than damage wrought by logging.

Redford investigated the truncated trophic cascades created by human harvest of animals in Amazon rain forests. These stands look deceptively dense and jungle-like, but when one looks closer it becomes apparent that they are empty.

Animal removal, termed *defaunation*, can be direct, by hunting or habitat destruction, or indirect, by harvesting of the fruits wildlife need for survival. Both occur regularly throughout Latin America. Redford estimated that in Brazil human subsistence hunters remove 14 million individual mammals per year. Current hunting is much higher than it has been historically because of the market for bush meat (wild meat). Hunters harvest monkeys and other jungle animals to meet the high food demand in logging and mining camps, driving to near extinction the large predators and herbivores that perform the important role of seed dispersal. Redford described the resulting forests as composed of "living dead" tree species, which will die without replacement. The harvested animals' absence truncates food chains and also reduces seed predation, herbivory, pollination, and predation on other animals. In Amazonia a forest open to hunting contains carpets of seedlings so thick that intense competition prevents all but a few from surviving, as well as piles of uneaten, rotting foods and ungerminated seeds. In contrast, a forest without hunting contains recruiting trees of large-fruited species, complex stand structure, and intact food webs.[5]

In southeastern Peru's Río Manú floodplain, John Terborgh and colleagues assessed how hunting alters recruitment of trees into tropical forest canopies. He compared Boca Manú, a site where large vertebrates had been overhunted, with Cocha Cashu, a reserve that contained intact fauna. Boca Manú species that had been greatly reduced included arboreal seed dispersers, such as spider monkeys (*Ateles* sp.), howler monkeys, and white-faced capuchins (*Cebus capucinus*), and terrestrial seed predators, such as collared and white-lipped peccaries (*Tayassu tajacu* and *T. pecari*). Terborgh measured sapling recruitment, seed dispersal, and the prominence of large-seeded species among those that showed impaired recruitment. He found few tree species populations that were stable, with 75 percent decreasing. Over time removal of animals is likely to diminish biodiversity, but this trend may be reversible if hunting is prohibited. Terborgh's research demonstrated that vegetation change in response to altered animal communities represents a serious threat to biodiversity, particularly because these effects may be subtle at first and difficult to detect without systematic surveys of plant and animal communities, until an ecosystem has passed a tipping point into another phase state.[6]

Pacific Northwest Forests: From Sustained-Yield to Old-Growth Conservation

A temperate old-growth rain forest is among the earth's most species-rich systems. However, this diversity is not uniform. Some taxa are rich, and some are not. For example, temperate old growth has few tree species but lots of fungal species, the reverse of tropical forests. High influx of nutrients and high standing crops of trees support this diversity, as do old-growth physical characteristics, as we shall see.

Just as a coral reef provides the structure and home for myriad species, in the Pacific Northwest the Douglas-fir (*Pseudotsuga menziesii*) serves a similar function, so much so that eminent forest ecologist Jerry Franklin and others refer to it as a keystone species.[7] While this designation does not strictly fit Robert Paine's definition of a keystone (i.e., a carnivore), this tree undoubtedly defines Pacific Northwest rain forests. Not a true fir, but rather the largest member of the pine family, the Douglas-fir has a colorful taxonomic history. Its genus name, *Pseudotsuga*, meaning "false hemlock," refers to the fact that early botanists misclassified it. This fast-growing generalist species ranges from southern Mexico to central British Columbia, growing from sea level to 9,000 feet. One of the most fire-hardy conifers due to its thick, corky bark, it has flat needles that are irregular in length and large cones with distinct scales that end in three-pointed bracts. Its branches grow in whorls tipped by sharp-pointed buds. This generally shade-tolerant species can regenerate in the understory of other trees, including pines. A formidable giant, it can grow to 300 feet and live for more than 1,000 years.

A Douglas-fir's high, multilayered canopy, thick bole, and enormous biomass, whether it is living or a snag, provides home for many organisms, such as the Douglas squirrel (*Tamiasciurus douglasii*), which harvests great quantities of cones, and the northern subspecies of spotted owl (*Strix occidentalis caurina*), which nests in broken-topped trees and in cavities abandoned by other birds. Remove the "keystone" Douglas-fir and the system ceases to exist as we know Pacific Northwest rain forests, although in time you might still end up with a coniferous forest made up of other species, with quite a bit of old-growth structure. Douglas-fir also yields more timber in the United States than any other tree, which adds another dimension to our human relationship with it. If you drive through Washington and Oregon you will see rows of young Douglas-firs growing vigorously in privately owned cutover lands west of the Cascade Divide, waiting to be harvested.

In any discussion of food webs in temperate forests, it helps to begin with the concept of old growth and consider how it arose and what it has come to mean to science and conservation. For eighty years forest management in the United States was based on sustained yield, a silviculture style developed in Europe in the mid-1800s. Brought to this country by Gifford Pinchot, the first chief of the US Forest Service (USFS), it called for growing trees as crops and harvesting them sustainably. This meant establishing a logging schedule based on the time it took for new trees to grow and replace the harvested trees. In the Pacific Northwest, the first half of the twentieth century was one of stewardship by the Forest Service because private interests did not want federal timber in the marketplace as they cut their own holdings. At this time old growth was the leading forest type targeted for logging because of its profitability. After World War II the federal timber era took off and old-growth harvest escalated, with an emphasis on sustained yield, despite environmental policy. But by the 1970s growing ecological awareness and unease about the conservation status of our natural resources led us to reevaluate the sustained-yield model and the principles we were using to manage forests.[8]

Early ecologist Frederick Clements' concept of succession and the climax community provided the theoretical foundation for sustained yield. His ideas created the dominant model for how ecosystems functioned until Charles Elton came along with an alternative perspective. In the 1920s Clements proposed that without human intervention, succession, or natural progression from one ecological stage to another, drove community dynamics. After a disturbance such as fire, flooding, or glaciation, all communities strove to the end point in their development, also referred to as the climax or equilibrium state. Climax communities, in which individuals are replaced by others of the same kind, are relatively stable. They feature a wide diversity of species and complex food webs. Clements suggested that succession to the climax was a predictable outcome and that climate (i.e., the recession of the glaciers) had an important role in this dynamic.[9] Additionally, he depicted succession as a universal process that creates patterns in the composition of any type of forest. Clements' ideas are quite valid today, but they explain only part of what drives community ecology. Today we know that the development of a forest from one stage through the next, via succession, provides a guiding force that shapes this system alongside other factors, such as trophic cascades.

Since understanding succession is foundational to understanding forests, let's follow a typical forest along its successional development. Each forest type, such as eastern hardwood or boreal conifer, has its own succession pathway, marked by certain species giving way to others. For example, after a stand-replacing event such as a wildfire, a pioneer forest of young Douglas-fir saplings comes up. This is referred to as an *early seral* community—an early stage in ecological succession as a community advances to the climax stage. It is also referred to as the *early successional* phase in the maturity of the stand, a time of heightened biodiversity due to resource availability (sunlight). The trees grow rapidly for several decades until the canopy begins to close, preventing light from reaching saplings on the forest floor, and biodiversity drops. Silviculturists refer to this as the *stem exclusion* phase. This enables species that are more shade tolerant, such as western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*), to sprout and thrive. Competition is a key aspect of this process, with certain organisms giving way to others on the basis of how much sunshine and moisture are available. Centuries pass, the long-lived Douglas-firs age and begin to die, and forest composition progressively shifts to other species, which eventually dominate the forest. As the forest matures further, biodiversity increases again because of increased diversity in stand structure. In the climax stage the forest primarily consists of western hemlock. The time required for succession from a young Douglas-fir stand to a climax hemlock forest can be as long as 1,000 years. Many forests never reach this stage because of disturbances that interrupt this process.

Clements' ideas about succession became popular during the 1930s, when the Forest Service was struggling to address economic problems caused by the Great Depression. We had been through other major upheavals, such as World

War I and the 1918–1919 influenza pandemic. Living in what appeared to be a deeply unstable, troubled world, people looked to science to help provide a path to stability.[10] Clements' ideas would influence timber harvest by supporting the notion that forests grow back after disturbance, allowing managers to reharvest this resource in an indefinitely renewable manner. But even back in the 1920s and 1930s alternative views existed.

British ecologist Charles Elton, who created the food pyramid and other seminal ecological concepts still used today, believed ecosystems were governed by complex interactions that worked alongside succession to create additional dynamics, such as the top-down effects of predators. In contrast to Clements' predictable succession patterns, Elton asserted that ecosystems were characterized by complexity, unexpected consequences, and the unimaginable—what today we refer to as *environmental stochasticity*. His ideas influenced Aldo Leopold, who as a 1940s resource manager pointed out the importance of acknowledging nature's uncertainty.[11]

In the 1970s the Forest Service continued to apply sustained-yield principles and considered ancient forests to be "decadent"—past their prime and far less productive than younger forests, which grew more vigorously. Nobody had yet defined the concept of old growth, much less recognized its ecological value. Jerry Franklin, then a young scientist on fire with new ideas about how forests worked, became the first to do so. His early work unfolded at the H. J. Andrews Experimental Forest, one of eighty-one forests set aside by the Forest Service for research purposes.[12] The science produced here would provide the wellspring of what became known as the "new forestry"—a more holistic approach to forest management. This progressive, ecosystem-based way of looking at forests would enable government agencies to incorporate growing knowledge about the effects of harvesting our natural resources and of natural disturbances on native ecosystems, too, such as the Mount St. Helens eruption. It led to the policy of ecosystem management, as part of the Forest Service's New Perspectives program in the early 1990s, and today may be informing the way we manage keystone species on public lands. We will explore ecosystem management further and its application within a trophic cascades framework in chapter 8.

Long-Term Ecological Research: The H. J. Andrews Experimental Forest

The H. J. Andrews Experimental Forest (HJA) is part of a network of living laboratories established by the Forest Service. Founded in 1948 and located fifty miles east of Eugene, the HJA encompasses 16,000 acres deep in the Oregon Cascades, in the Blue River drainage of Willamette National Forest. It ranges from 1,380 to 5,350 feet in elevation. Douglas-fir and western hemlock dominate its lower regions, along with western red cedar, with Pacific silver fir (*Abies amabilis*) growing at higher elevations. Lookout Creek, a tributary of the Blue and McKenzie rivers, runs through this watershed, its clear waters providing habitat for cutthroat trout (*Oncorhynchus clarkii*) and the coastal giant salamander (*Dicamptodon tenebrosus*). The Forest Service's Pacific Northwest Research Station, Oregon State University, and Willamette National Forest administer this forest jointly, with a history that includes Jerry Franklin, Frederick Swanson, and most recently Barbara Bond as principal investigators. Natural history writer and lepidopterist Robert Michael Pyle referred to the HJA as a place where "when a tree falls in the forest, a lot of people hear it—and then take a close look at what happens next."[13] Part of the National Science Foundation's Long-Term Ecological Research (LTER) program since 1980 and a UNESCO Biosphere Reserve, the HJA has led forest ecosystem research for decades.

The LTER network comprises twenty-six sites, mostly in North America, with one in Antarctica and another in the western Pacific on non-US territory, that exemplify a wide range of ecosystem types, from kelp forests to urban landscapes. At each site scientists focus on five core research areas: primary production, distribution of populations selected to represent trophic structure, accumulation of organic matter, nutrient movement, and disturbance. At the HJA the overarching question has to do with how land use, natural disturbances, and climate variability affect key ecosystem properties. Addressing this requires research that potentially spans several generations of human lives, that is, the time it takes for a log to decompose or a young forest to develop into an old-growth stand.

Ecologist Mark Harmon's log decomposition study, which is taking place on a monumental scale, exemplifies this long-term approach. Since 1985 he has been studying how trees rot in this forest, in plots that he intends to be surveyed beyond the next century by generations of future ecologists. Operating under the assumption that each log can be considered an ecosystem on its own because of the amount of life it sustains, Harmon suggests that these relationships continue long after its death, until it has become transformed into other states, such as soil carbon, organic matter, or gas—in other words, until it has decomposed beyond recognition as a log. To quantify this he is measuring the amount of carbon dioxide a decomposing log gives off and the nutrients, insects, and fungi it harbors, as well as its hydrologic function as a water reservoir on the forest floor.[14] HJA studies such as this aim to increase understanding of the ecological function of old growth. As Pyle put it, "The long view requires faith in the future—even if you won't be there to see it for yourself . . . looking to the future is a way of hoping there will still be something to see when we get there. Maybe it's the only way to make sure of it."[15]

Much of what goes on in old growth takes place in the hidden forest: the soil. For example, *mycorrhizae* are fungi that form a symbiotic relationship with the roots of a plant. Trees provide them with nutrients in the form of carbohydrates from photosynthesis. In exchange these fungi act as extensions of the tree's root system, aiding its uptake of water, nitrogen, and phosphorus. Food web processes such as these are vital to forest health.[16]

In the 1970s James Trappe, a fungus expert, and Chris Maser, a mammalogist, discovered a mutual relationship between the endangered western red-backed vole (*Myodes californicus*), truffles (*Tuber* spp.), and Douglas-firs. Truffles are underground versions of mushrooms, the "fruit" of the fungal mat created by mycorrhizae. Roughly round and brown, they resemble small potatoes and range from one-half to three inches in diameter. Because they grow entirely belowground, they can disperse their spores only by being eaten, in a process called *mycophagy*. The red-backed vole subsists almost entirely on truffles, which also provide an important food source for other animals, such as the northern flying squirrel (*Glaucomys sabrinus*) and even mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*). These animals eat the truffles, in this manner dispersing spores essential to the growth of Douglas-firs and other conifers.

And when a Douglas-fir dies and falls to the ground, it rots, creating a nutritious medium for truffles to grow in, completing this cycle.[17]

Disturbance, which influences every aspect of a forest, including food webs, provides another leading research topic at the HJA. Frederick Swanson has spent a lifetime studying disturbances ranging from the 1980 Mount St. Helens volcanic eruption to landslides in forest streams. Tall and lanky, he has a full beard and the sharp eyes of one who notices and carefully considers everything. When he speaks about disturbance his face grows animated and he starts gesturing with his hands. He began his HJA work in the 1970s with a new PhD in geology, doing a postdoctoral study with Franklin on how disturbance affects landform development. From the start he saw the HJA as a dynamic ecosystem where mountains, trees, and streams were always moving, sometimes slowly, sometimes in catastrophic bursts, as in the sudden flow of muddy debris after a long rainstorm. Debris flows can occur as a result of exceptionally heavy rainfall, which causes streams to rise. Generally debris flows start as saturated soil breaks loose from hillslopes and cascades downslope, into steep streams, and then down the river channel. The resulting torrent breaches natural dams, moving dirt, rocks, and fallen trees down hillslopes and streams, scouring the channel. This can widen a stream, causing large changes in the landscape and plant communities. In 1996 heavy rains and snowmelt sent giant logs and boulders hurtling down Lookout Creek, providing a tremendous opportunity for Swanson to observe these geomorphic dynamics up close. Over the years he has broadened this work to include volcanic activity in far-flung places, such as Chile, and other disturbance types, such as fire and windstorms, and has also become engaged in policy work related to forest management.[18]

The Guru of Old Growth

The 1970s and 1980s were exciting times at the HJA, with Franklin assembling an interdisciplinary team to conduct cutting-edge research on forest science topics that ranged from disturbance to nutrient flow. Currently holding an endowed chair, and a professor of ecosystem analysis at the University of

Washington, he is referred to as the "guru of old growth" because of how his revolutionary science has changed forest management over the years. On a warm, humid midsummer day in 2009 I took a walk in the woods with him in Olympic National Park, along the South Fork of the Hoh River. We followed a trail through one of his favorite groves of centuries-old spruce and fir, discussing his early work at the HJA and the intricacies of food webs in this forest. Winter wrens' lilting melodies echoed through the understory created by the giant trees, providing a backdrop for our conversation. A veteran forest scientist, Franklin knew these woods well and moved easily through them as he showed me the complexities of old growth. And as we explored this stand we became engaged in a lively discussion about the likelihood and unlikelihood of trophic cascades in this system.

Franklin has always been drawn to uncharted terrain. In the early 1970s, supported by the National Science Foundation, he turned his full attention to old growth. Until then no formal definition of this forest type had existed, yet emerging forestry practices required that managers set some old growth aside.[19] To that end he convened the HJA researchers and led them in creating a monograph titled *Ecological Characteristics of Old-Growth Douglas-Fir Forests*. Published in 1981, it would provide the basis for policy that transformed traditional forestry. Franklin and his colleagues proposed that old-growth forests differ significantly from younger ones in species composition and in the ways they function, that is, rate and paths of energy flow, nutrient and water cycling, and physical structure.

Four fundamental structural components create an old-growth forest's complexity: large live trees, many snags, and logs on the ground and in streams. In their report Franklin and his colleagues referred to old growth as far more than a collection of large, decadent trees. They saw dead, decaying organic matter as an important resource, to be maintained for the ecosystem benefits derived from it, such as enhanced nutrient cycling and fish habitat. Additionally and most radically, this report proposed an ecosystem approach to resource management, one in which managers recognized the interlinked nature of forest components, which included organisms and their functions. In this scenario, successfully managing old growth meant avoiding salvage logging after a wildfire, to allow snags to remain standing and provide a home for wildlife. The HJA team recommended that even within a multiple-use framework, managers acknowledge the nontimber value of individual trees. They also suggested maintaining trophic interactions among species at all structural levels.[20]

In the decade that followed, Franklin and a core of researchers, including Frederick Swanson, stream ecologist Stanley Gregory, and others, worked hard to define patterns and processes in old-growth forest. Gregory began his work here in the 1970s, first studying primary productivity (energy flow driven by sunlight, moisture, and photosynthesis) in streams. Later he began investigating the role of logs in streams and the interface between riparian areas and land. He saw streams as three-dimensional interaction zones bounded by a river's floodplain and the forest canopy, with disturbance creating a variety of habitats, determining the abundance and quality of nutrients, and influencing trophic relationships.[21] Also, he led production of a stream and riparian management guide for the Willamette National Forest plan of 1990, which became a foundation piece for later conservation strategies, such as the Northwest Forest Plan. This and other benchmark research helped people begin to see ecosystems in new ways, to the extent that in the 1990s the HJA would be the epicenter of one of the most intense environmental controversies in US history.

The Northern Spotted Owl and the Northwest Forest Plan

Research on the northern spotted owl (*Strix occidentalis caurina*) began in the 1970s, led by Eric Forsman, a master's student, working in the HJA and in neighboring forests. Endemic to the Pacific Northwest, this subspecies of the spotted owl has white spots on its head, neck, and back; brown bars on its chest and abdomen; and big, dark eyes set into a prominent facial disk. It nests in the tops of old trees and snags, mates for life, tolerates disturbance poorly, and feeds primarily on wood rats (*Neotoma* spp.) and flying squirrels.[22]

In the 1980s Forsman was the first to determine this owl's habitat needs: old-growth forest, a community type that by then had been reduced severely in the Pacific Northwest.[23] Habitat fragmentation and reduction caused the northern spotted owl to be placed on the list of species to be considered for government protection. Conflicts escalated on federal lands over protecting its habitat, which meant reducing timber harvest. In 1989, in response to growing concerns, the federal government asked wildlife ecologist Jack Ward Thomas, who later became chief of the Forest Service, to create an independent scientific plan for the owl's recovery. For political reasons, which included impacts on timber harvest, the plan was never formally approved; however, in 1990 the federal government listed the owl as threatened under the Endangered Species Act (ESA). In 1991 Congress chartered the Scientific Panel on Late-Successional Forest Ecosystems to develop multiple alternatives for this subspecies' conservation. The panel's four principal scientists, who came to be called the "Gang of Four," were Thomas, Franklin, forest policy expert K. Norman Johnson of Oregon State University, and John Gordon of Yale University.[24] To meet ESA criteria for population viability of wildlife dependent on old growth, in 1993 the Forest Service drafted the Northwest Forest Plan (NWFP). This statute took an ecosystem approach to forest management using the best available science.[25]

According to Thomas, in the five years between 1989 and 1994, as a result of changing environmental policies to protect old growth, management objectives on public lands within the spotted owl's range shifted dramatically from sustained yield of timber to maintenance of biodiversity, with an emphasis on endangered species.[26] This resulted in wholesale reduction of logging of old-growth forests. Much of the remaining old growth was designated for protection in *late successional reserves* on 24 million acres in the Pacific Northwest under the Northwest Forest Plan. Almost overnight timber yield plummeted by 80 percent, although in practice it may have been more like 90 percent.[27] Johnson has referred to this as a no less catastrophic regime shift than the Mount St. Helens eruption. It involved an abrupt transition from Pinchovian forestry to the holism of the "new forestry," with this owl the flagship species for old growth. This precedent-setting conservation story provides a compelling example of the relevance of taking an ecosystem approach. And it opened the door for future science-based resource management, such as policies involving keystone species (e.g., gray wolf reintroduction), which we will examine in chapter 8.

Another Empty Forest?

We have seen how the absence of large mammals in tropical rain forests left plant communities simplified. Now let's examine how these effects may be functioning in the Pacific Northwest from the perspective of wolf (*Canis lupus*) conservation. Humans had effectively removed wolves from Oregon by the mid-1940s because of fear of how they would affect livestock and elk and deer populations. However, by the late 1990s wolves had begun returning from Idaho. In 1999 a radio-collared female arrived in the eastern part of the state, and in 2008 the Oregon Department of Fish and Wildlife confirmed wolves denning there.[28] As of 2009 wolves were not known to exist at the HJA, in central-western Oregon; however, given their peripatetic nature, it may be only a matter of time before they recolonize this general area as well.

Like many western states, Oregon has a long-standing reputation for abundant wild game. While what we know about historical elk numbers is somewhat speculative, it appears that they were high in the early 1800s but had declined by the end of the 1800s as a result of overhunting by humans. As a result, in 1899 the state legislature responded by making it illegal to sell wild animal meat, banning elk hunting from 1909 to 1932. In the 1930s this species' population began to increase, very likely because of hunting restrictions and predator extirpation as well as logging, which improved habitat by creating forest openings filled with browsable sprouts.

The HJA harbors a wealth of invertebrates but low numbers of large mammals. Oregon has two native subspecies of elk: Rocky Mountain elk (*Cervus elaphus*), which inhabits the eastern part of the state, and Roosevelt elk (*C. elaphus roosevelti*), which lives in rain forests. Current elk presence in the core of HJA old growth is negligible because this species tends to prefer open habitat, such as logged areas, and the edge, or ecotone, between forest and grassland. The elk population in what is now the HJA may have been higher when that area was a younger forest, but as in other areas, we have insufficient archaeological information, such as remains of human encampments and fire circles containing elk bones, to be certain. Other large mammals currently here include mule deer (*Odocoileus hemionus*), coyotes (*Canis latrans*), cougars (*Puma concolor*), and black bears (*Ursus americanus*). Cougars and bears exist in low densities, but even with these carnivores present, the resulting food web has been truncated in an area that once held a wolf population. Historical references, such as the predator surveys conducted at the turn of the century by US Bureau of Biological Survey biologist Vernon Bailey and others, provide ample evidence of wolf presence here. And these historical reports make one wonder what this place might have been like when it had an intact predator guild.[29]

I spent some time on a cold, cloudy spring day walking through the old-growth forest near HJA headquarters with Swanson and hydrologist Julia Jones, discussing this question. Both know this forest with an intimacy born of years of research. Jones studies stream flow response to forest harvest and landscape-scale disturbance patterns. Petite, with wavy brown hair and an infectious smile, she has made major contributions to the research in this forest. And so I was well accompanied as we set out to look for trophic cascades. In the absence of any formal research on the food web effects of large mammals here, we discussed the possibilities. While our conversation that day amounted to little more than conjecture, the idea of missing fauna and the changes this might have caused in plant communities intrigued us.

Swanson led us into the forest on a narrow, snow-packed trail. He clambered over the massive, mossy trunks of fallen Douglas-firs in our path, moving with the speed and agility of one who knows this landscape well. As we walked I examined the vegetation, which did not appear to be suffering from too much herbivory, because elk and deer numbers were low. But taking a longer view, Swanson suggested that the apparent absence of a strong trophic cascade at the HJA may be a reflection of today's forested landscape, which includes the properties of an old-growth forest, such as great structural and species diversity, as well as its properties on a longer time scale (millennia), which have to do with this system not having a tipping point between phase states, the way a kelp forest or a forest-grassland system in Yellowstone National Park does. However, in considering old-growth dynamics, he suggested that there may be periods when a cascade could have occurred here—for example, in the immediate aftermath of an extensive, severe fire.

Elk follow fires because a high density of tender, nutrient-packed shrub and tree sprouts come up during the first few years after a fire. This may explain why HJA forest ecologists, who have found a connection between tree regeneration and site disturbance histories (e.g., wildfire, defoliation of Douglas-firs by insects), have been observing a historical lag (approximately forty years) in tree establishment following disturbance, on the basis of tree ring data that goes back to the 1500s, with some data going back to the 1400s and 1300s. This lag could possibly have left some time for expansion of elk herds in the early seral periods of the early 1500s. Other factors that may influence a trophic cascade at the HJA include differential browsing pressures on plant species, based on their taste appeal to ungulates, and the time necessary for an ungulate population, which may normally be low in old growth, to increase after a disturbance in order to capitalize on enhanced resource availability.

As in other places, it's likely that removal of large carnivores may have left broad, landscape-scale marks on this forest via trophic cascades. However, our understanding of how this may have worked in this ecosystem remains uncertain. Swanson emphasizes the need for researchers to develop a general conceptual model of these interactions—one that incorporates potential effects of the logging and broadcast burning prevalent in the early 1900s, as well as other forms of human-caused disturbance, including aboriginal use of resources. Ideally this model of vegetation change and trophic cascades would, like most of the work being done at the HJA, employ a long-term, multicentury approach. Accordingly, it would consider natural and human influences on distribution of early seral habitat. This forest type has waxed and waned in distribution over the past five hundred years for which we have spatially explicit records.

Additionally, Franklin and Swanson suggest that it's likely that a Douglas-fir–western hemlock forest may lack a keystone predator, as in simpler systems with shorter successional pathways. While wolves may have historically exerted a top-down influence in some localized areas on a limited time scale, with disturbance a factor (i.e., disturbance creating forest openings, which draw ungulates, which then draw predators) and plant community patterns reflecting this, overall it is unlikely that a top predator would have the same sort of controlling influence on the whole system as it does in the northern Rockies in aspen communities. Part of this may be because of the nature of Douglas-fir–western hemlock successional dynamics. At any rate, it would be important to science to investigate these dynamics.[30]

Old-Growth Reflections: The Spring Creek Project

In addition to world-class science, the HJA also fosters innovative cross-disciplinary work. Swanson's view of this place as more than the sum of its parts has helped create a fruitful collaboration with the Spring Creek Project. Affiliated with Oregon State University and directed by philosopher Kathleen Dean Moore and poet Charles Goodrich, this program brings together environmental sciences, philosophy, and writing to find new ways to envision our relationship with nature. This approach is as relevant today as it was in the 1930s, when Aldo Leopold (a writer and scientist) and Olaus Murie (a painter and scientist) used the arts to inform their scientific work. At the HJA, the LTER program and Spring Creek's Long-Term Ecological Reflections program create regular opportunities for writers and scientists to work interactively in the forest and tap into each other's wisdom, yielding a rich body of writings and insights into old growth. The funding for Reflections comes from Forest Service research funds and from the Spring Creek Project. The Forest Service's role in supporting this work is part of the agency's responsibility to manage these places dedicated to learning. Emerging themes in the poetry and essays being produced at the HJA include the importance of taking the long view, the critical role of language, especially metaphor, and how the synergy between science and the humanities can help sustain ancient forests. This cross-disciplinary approach can produce a heightened awareness of relationships in the natural world, such as the ecology of fear, and why it matters.[31]

One recent autumn I participated in a program at the HJA. Moore and Goodrich gathered poets, novelists, and essayists from throughout the West to discuss our calling as writers in this time of rapid global change. Over a three-day period, we spent as much time as possible afield, enjoying the luminous late September days. Sitting in a hemlock stand at one of Harmon's log decomposition plots, Swanson taught us how to "read the forest," interpreting stories trees can tell us about earlier events, such as fires, windstorms, and floods. As we shared our writings and impressions about the nature of this forest, Swanson lay down on the moist, mossy ground and gazed up at the canopy far above, his face filled with wonder. Moore sat cross-legged at the base of a hemlock, eyes shut, a blissful expression on her face. Ancient forests have tangible (economic) and intangible (aesthetic) values. That this forest can inspire awe in a scientist who has studied it for decades and can give wings to philosophical ideas about science, the humanities, and relationships in the natural world illustrates its intangible value.

As Goodrich read us Tang Dynasty poems that probed the dark, damp depths of ancient forests, I leaned back against a Douglas-fir and recalled my first trip to the HJA in 2007 as a visiting scholar. By then I was a graduate student in forestry and wildlife with field experience in various other forest types. It was early spring as I walked into an area referred to as Watershed One. Everything was green, even the bark on shrubs, covered with a fine moss. What struck me first about this viscid, verdant place was its multiple spatial scales—from the very large (a 300-foot Douglas-fir) to the minute (droplets of water embedded in the tree's corked, mossed bark). The trees' immensity and my awareness of this forest's age were humbling. Some of the oldest trees in this stand had originated 500 years ago, after a major fire. Sunlight filtered through lacy hemlock boughs, suffusing the understory with a low green light. Other than the song of creek water on stone and the soughing of the wind in the canopy, this place seemed preternaturally silent—I didn't even hear birds or squirrels. I walked on forest trails amid moss-veiled yews, the earth spongy underfoot from millennia of decay. The bones of long-dead trees lay strewn about this landscape, which had been created by the pit-and-mound architecture of decay. Life and death merged seamlessly, with deadfall acting as nurse logs to young saplings, all part of the same continuum.

This place was filled with the contrast of old and new. Artifacts of the state-of-the-art research being conducted here by ecologist Barbara Bond—metal towers, sensors, cables, antennae, and white plastic pipes—rose incongruously from the ground. In one of the most ingenious projects taking place at the HJA, she was documenting how the forest breathes, tracking the miraculous daily movement across this mountainous landscape of what literally amounted to a river of air. Each day the trees breathe, as part of the carbon cycle, pulsing energy through the food web. To learn more about how forests function, Bond followed the nighttime movement of cold air through this landscape with a wireless electronic sensor network designed for this project.

As I walked farther, I wondered how science can do justice to this complex, ancient community. Long-term ecological reflections mean acknowledging that we can't find full answers to ecological questions—including those about trophic cascades—without looking deep and long. LTER sites like the HJA offer places where one can slow down and look at things at the speed of rot. Long-term ecological research entails compiling generations of data, layers of learning, to yield some understanding of the holistic functioning of old-growth forests. Year by year the data accumulate, like leaf litter on the forest floor, each observation contributing to the whole of our knowing, helping us to redefine who we are in relation to the world. Such has been the incredibly fertile research legacy created by Jerry Franklin and carried on by Swanson, Bond, and their many colleagues. Scientists who work in this forest know that there is much more here than we will ever know. Moore, Goodrich, and Swanson are giving them and those involved in the humanities the opportunity to reflect on these matters more deeply.

The Wind River Experimental Forest: Canopy Cascades

My field time as a visiting scholar at the HJA led me to another site to search for trophic cascades in a less accessible part of a forest. Established in 1932, the Wind River Experimental Forest is referred to as the "cradle" of forest research in the Pacific Northwest. This unique facility has a canopy crane, which would enable me to explore food webs in the crowns of old-growth Douglas-firs. It lies in Washington's Cascade Range, in Gifford Pinchot National Forest, eighty miles from the Pacific Ocean. Administered by the Pacific Northwest Research Station in Portland, Oregon, it is one of ten experimental forests within the station's jurisdiction (Oregon, Washington, and Alaska). Additionally, in the early

1900s the Forest Service established research natural areas (RNAs) to represent different types of terrestrial and aquatic ecosystems.[32] The Thornton T. Munger RNA, created in 1926, lies within the Wind River Experimental Forest and contains an old-growth Douglas-fir–western hemlock stand. This cool, moist 500-year-old forest has a mild maritime climate and lies in the transition region between the Coastal Western Hemlock Zone and the Pacific Silver Fir Zone, which occurs above 2,900 feet.[33]

Wind River research concentrated on silviculture through World War II and into the 1970s. In the 1980s the focus shifted to ecosystem studies and relationships of old growth and wildlife habitat. Jerry Franklin, who left the HJA for a sabbatical at Harvard University in the mid-1980s, became the Wind River plant ecologist shortly thereafter. He had spent considerable time in that area as a child growing up in western Washington and thus had a connection to this landscape. In 2007 the National Science Foundation designated the Wind River Experimental Forest one of twenty core sites in the National Ecological Observatory Network (NEON). This program uses cyber-technology, such as environmental sensors, to support interdisciplinary, collaborative research on how environmental changes are affecting forests and biodiversity.

When I arrived at Wind River in late March, several feet of crusty snow covered the ground. It was thirty-five degrees and raining steadily—the sort of rain-on-snow downpour typical at this time of year. I built a fire and made tea in the historic Forest Service cabin where I was housed. As I brought in wood at dusk, I discerned the shadowy forms of elk grazing in an open field (a former tree nursery) across from the cabin and heard a varied thrush's buzz song echo through the forest. Alone in this beautiful, rustic cabin, I spent the evening listening to the drum of rain on the shingle roof and reading about this research facility's more recent history.

In the 1970s HJA botanist William Denison, who insisted that you can't understand forest ecology without looking at what goes on in the treetops, pioneered canopy studies at the HJA. His work inspired vital research by Nalini Nadkarni, Margaret Lowman, and others. In 1980 the Smithsonian Institution installed the first canopy crane in Panama. Prior to that researchers had to use climbing gear (rope) and rock-climbing strategies to access the forest top.

Fourteen years later Jerry Franklin had a crane tower erected at Wind River, and he has been director of this research facility since then, with the assistance of David Shaw during the first decade and Ken Bible more recently. Identical to those used to build skyscrapers, the crane carries an eight-person gondola, has a 279-foot jib, and is as tall as a twenty-five-story building. It offers access to a cylindrical volume of more than 54 million cubic feet, which contains 300 trees. Researchers study such topics as carbon, water, and nutrient cycles; tree physiology and growth; climate variability; the relationship between biodiversity and ecosystem functions; and lichen and fungal ecology.

I rose at dawn the next morning to prepare for my trip into the canopy. The rain had ended overnight, fog blanketed the forest, and the temperature had dropped into the twenties, coating everything with ice. I put on extra wool layers. My companions that day included site director Ken Bible and research scientist Matt Schroeder. They planned to install sensor buttons on trees to gather temperature and humidity data in order to measure habitat variation and its effect on growth and canopy organisms. After donning nylon safety harnesses and hard hats, we stepped into the gondola basket and clipped ourselves to the railing. As the electric-powered crane silently propelled us into the dark, still canopy, we entered another world—one seldom seen at arms' length by humans. More smoothly than any elevator ride I had ever taken, crane operator Mark Creighton expertly lofted us through the lower canopy and into the forest nave and upper canopy. As we rose beyond the cone zone on this quintessential Pacific Northwest spring morning, I could see that the fog was already dissipating. A panoramic view opened of low volcanic mountains densely carpeted with forest, ridgelines fading into shades of distance. The previous night's storm had left everything green and growing, wet on wet, in infinite shades of green. The sun burned through the low clouds and made the icy raindrops that clung to the treetops glitter like crystals.

The crane stopped and left us looking down on the interwoven crowns of ancient trees. My strongest impression was of immense structural and textural diversity. While I had studied canopy structure in silviculture textbooks, which featured tidy diagrams depicting multiple levels of trees, this was the first time I had physically explored this structure. More than simply a collection of treetops, the canopy encompasses all the living (biotic) and nonliving (abiotic) components of trees, such as atmospheric gases and tree litter.[34] Although its medium was air rather than water, the canopy most resembled a coral reef in terms of its structural complexity and the wealth of life it held, including many insects, birds, and lichens. And as I looked I noticed a lacy lichen liberally distributed among the branches in the upper canopy.

The lichen *Lobaria oregana* is composed of lime green, frilled, and veined lettuce-like leaves, which sometimes resemble elephant ears. Primarily growing in ancient forests because of its light and moisture requirements, *Lobaria* accounts for up to half of the foliar biomass in lowland Douglas-firs. It is part of a class of nitrogen-fixing lichens termed *cyanolichens*, which harbor nitrogen-containing bacteria. Rain washes off the bacteria and leaches their nitrogen into the soil, making it available to trees and other plants. *Lobaria* is scarce in young forests, which provide insufficient shade for this genus. Lack of cyanolichens in cutover second-growth forests diminishes the amount of nitrogen cycled through these systems.[35]

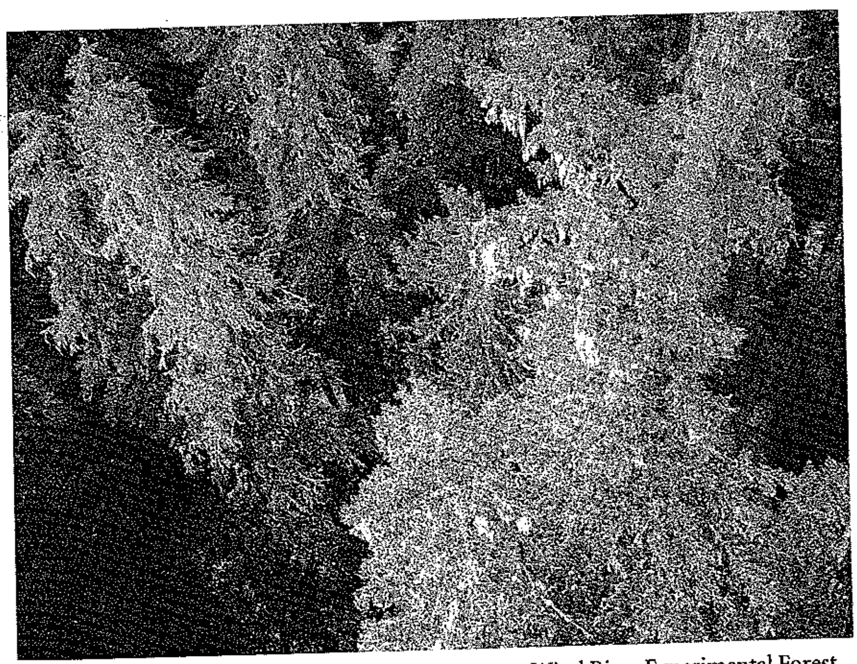

Figure 5.1. Old-Growth Douglas-Fir–Hemlock Canopy, Wind River Experimental Forest

The canopy's complex structure creates *microsites*—small, discrete patches of habitat, stratified by elevation and related to the amount of light and moisture that reaches them. Some species prefer certain portions of the canopy. For example, the red tree vole (*Arborimus longicaudus*) uses the lower canopy of the largest trees in old-growth forest. It spends all its life aboveground, where it disperses spores and seeds and provides a valuable food source for predators. Some songbirds, such as the brown creeper (*Certhia americana*), forage selectively. Most of the year this species harvests insects from tree bark in the midcanopy, but in spring it shifts to the high canopy.[36]

Canopies undergo development over time, as is most apparent in old-growth forests, which feature a variety of structures, from the tender green, rapidly growing tops of young hemlocks to the broken, gnarled crowns of ancient Douglas-firs. This parallels the succession pathways discussed earlier in this chapter, caused by competition for light, which drives structural changes in trees, and also by disturbance, which creates openings and enables shade-intolerant species to grow.[37] The canopy before me demonstrated all these processes at once, and it took me the several hours I was up in it to begin to explore its richness. The crane provided the ideal vehicle for this as it glided from tree to tree and level to level.

While Bible continued positioning sensors, I looked for trophic cascades, curious about whether canopies contain some of the food web relationships I had been observing elsewhere. He and Schroeder inspected the tops of hemlocks severely infested with dwarf mistletoe (*Arceuthobium tsugense*), a small, brownish, leafless parasitic plant. When I asked what was causing this outbreak, they said it was due to an exceedingly rare butterfly that lays its eggs only in the tops of mature hemlocks—or, more accurately, due to its lack.

In 1952 Ray Bradbury wrote a short story, "A Sound of Thunder," about how a butterfly had far-reaching effects that rippled through time. In this story a time traveler ventured to the dinosaur era. The scientist who operated the time machine warned him not to disturb anything. As he walked in a Jurassic rain forest the traveler inadvertently killed a butterfly by stepping on it. Upon returning to the present, he found things significantly different—language, political regimes, how the world looked. In science, the notion that a small organism's status and actions can have profound effects came to be known as the *butterfly effect*.[38] As Bible and Schroeder described what amounted to a butterfly effect in this forest, I began to piece together its trophic implications.

The Johnson's hairstreak (*Callophrys johnsoni*), which has been observed in the canopy at Wind River, also commonly known as the mistletoe hairstreak, is a one-and-a-half-inch olive green butterfly marked with brown, orange, or blue spots and a white zigzag on the underside of its wings. Other field marks include double tails and raised dorsal chevrons. According to Robert Michael Pyle, it is the only old-growth obligate butterfly, which means it requires ancient forests to survive. It lays its eggs only on dwarf mistletoe, which the caterpillars eat when they hatch. According to the Xerces Society for Invertebrate Conservation, this butterfly once occurred from southern British Columbia south through eastern and western Washington, Oregon, and western Idaho to central California. It probably existed throughout much of western Washington's old growth prior to 1900. It has severely declined as a result of habitat destruction caused by logging and the spraying of insecticides to kill tussock moths and budworms in conifers. Other than relatively recent sightings in the Wind River Experimental Forest and Olympic National Park, it was last seen in 1969 in King County, Washington. Thus it's likely that when mature hemlocks abounded in the Pacific Northwest, so did the Johnson's hairstreak, keeping the parasitic dwarf mistletoe under control. And as logging depleted these trees, dwarf mistletoe was depleted as well, and this butterfly declined for lack of egg-laying habitat.[39]

The Johnson's hairstreak decline created an ecological chain reaction. Dwarf mistletoe lives in older hemlocks and survives by taking water and nutrients from its host. Too much mistletoe can severely damage a hemlock, impairing the tree's ability to circulate water and nutrients by as much as 50 percent. While most hemlocks survive light infestations, trees with heavier infestations are unable to compete with healthier trees for resources; those whose boles are infested eventually die. A heavy outbreak also greatly reduces a tree's ability to produce cones. Because the Johnson's hairstreak has become so rare, dwarf mistletoe is taking over many of the mature hemlocks in the Pacific Northwest, impairing their health. As these trees continue to decline, they have a lower likelihood of reproducing. Fewer hemlocks mean the decline of other species dependent on their cones for nutrition, such as common crossbills (*Loxia curvirostra*). Existing hemlocks' inability to adequately cycle nutrients reduces resources available for invertebrates and mycorrhizal fungi. And because all things are connected, this negatively affects soil composition, other tree species, understory vegetation, and wildlife.

While the Johnson's hairstreak butterfly can't be considered a keystone species as traditionally defined by Paine (it's not a carnivore), it is a strongly interacting species—one whose presence or absence has tremendous influence. These cascading effects show that food web connections, even involving small organisms such as this brown butterfly, can touch every member of a food web. And while today we know that the "balance" of nature is a myth because nature is filled with uncertainty and unpredictability, removal of a butterfly species can upset or sever evolutionary relationships and cause systems to change across multiple trophic levels.

Riparian Cascades in Temperate Rain Forests

Riparian studies have been part of old-growth forest science since this field's early years. In 1966, inspired by research in other systems, HJA scientist C. David McIntire created an integrated model of the major trophic levels of riparian food webs (e.g., detritivores, carnivorous and herbivorous fish).[40] In chapter 3 we learned about Mary Power's seminal 1980s trophic cascades work in northern California's Eel River. She has also studied how rivers subsidize watersheds in old-growth forests and found a trophic connection between the carbon produced by riparian food webs and insect abundance. In this study, which also took place along the Eel River, carbon indirectly increased numbers of insectivores, including lizards, birds, and bats, a bottom-up effect. In the 1990s HJA hydrologist Steven Wondzell took an even more holistic view, linking rivers and landscapes via nutrient flow in the hyporheic zone and examining the role of disturbance in shaping the resulting energy exchange.[41] Also, since the 1990s hydrologist Julia Jones and her colleagues have been studying differences in water use by hardwoods and conifers and how vegetation age, structure, and species composition affect hydrologic patterns in rivers.[42] In 1997 Robert Naiman, a specialist in Pacific Northwest riparian ecology, added another dimension by suggesting that a combination of herbivory by large mammals and other forms of disturbance, such as floods, shapes riparian areas by modifying vegetation distribution, and that keystone predators may have a role in this. Specifically, he identified the potential indirect trophic effects that wolves and river otters (*Lutra canadensis*) have on plant communities by influencing the abundance, distribution, and browsing choices made by their prey.[43]

Hydrologist Robert Beschta has long been aware of the ecological importance of riparian vegetation, which stabilizes riverbanks and controls the amount of light that reaches streams, thereby regulating water temperature. In 2008 he and William Ripple investigated a potential riparian trophic cascade consisting of wolves, Roosevelt elk, black cottonwoods (*Populus trichocarpa*), and bigleaf maples (*Acer macrophyllum*) on Washington's Olympic Peninsula—a large arm of land west of Seattle, across the Puget Sound. This rain-drenched landscape (about twelve feet of rain falls annually on west-facing valleys, making it the wettest place in the forty-eight coterminous United States) contains the Hoh, Queets, and Quinault rain forests, some of the most productive timberlands in the United States, as well as Olympic National Park. Roads provide access to the park's perimeter but not its primeval interior. The glacier-topped Olympic Mountains rise directly out of the Pacific Ocean and dominate the center of the peninsula, forming a cluster of jagged peaks rimmed by thickly forested foothills and valleys. Out of these mountains flow thirteen salmon-bearing rivers, which descend steeply, incising the timbered foothills as they course swiftly down to fertile valley bottoms, floodplains, and the Pacific Ocean.

As elsewhere, wildlife populations have left their marks on this peninsula's plant communities. Elk abounded here until 1895, when they were overhunted by settlers. In 1905 the federal government implemented a peninsula-wide hunting ban, causing elk numbers to surge, with heavy browsing reported by 1915. By the 1920s humans had extirpated wolves, which exacerbated the irruption, and in 1935 Olaus Murie reported that the excessively high elk population was depleting its food sources, including understory plants.[44] Congress created the park in 1938 to protect old-growth forests and elk habitat; however, without wolves and hunting by humans, intense elk browsing has continued through the present.

Also as elsewhere, wolves have begun returning to Washington, drifting down from southern British Columbia, where they were never fully extirpated, and also dispersing into southeastern Washington from Idaho. In July 2007 a pack denned and produced pups in Washington's Okanagan country in the North Cascades, approximately 100 miles east of the Olympic Peninsula. In 2008 a wolf was spotted in southwestern Washington, on the boundary of the Wind River Experimental Forest. There have been other sightings throughout the Washington Cascades, but as of 2009 no wolves had been reported on the Olympic Peninsula, possibly because of formidable geographic barriers, such as the city of Seattle and Puget Sound.

Beschta and Ripple examined food web effects in Olympic National Park—a protected area—and contrasted that to an area of multiple human land uses outside the park on the Quinault Indian Reservation. The overstory in their study areas consists of red alders, black cottonwoods, bigleaf maples, Sitka spruce (*Picea sitchensis*), western hemlocks, and western red cedars. In response to disturbances such as logging, fire, or flooding, these forests form dense shrub understories. Beschta and Ripple focused on the healthy growth of two common elk foods, black cottonwood and bigleaf maple, along the Hoh and Queets rivers inside the park. For comparison they used a bar on the lower Quinault River, outside the park, that had low elk presence as a result of human activity. At all but the Quinault bar they found a gap in cottonwood and bigleaf maple ages correlated to wolf extirpation, consistent with a trophic cascades hypothesis in which the abundance of a keystone predator (wolf) influences the abundance of its primary prey (elk), which influences plant communities (cottonwoods and maples). They attributed cottonwood and bigleaf maple recruitment on the lower Quinault to human activity and land uses such as hunting.

Franklin and other scientists agree that elk are a major ecological force shaping vegetation patterns in valley bottom old-growth forests in Olympic National Park. This has been documented in studies by ecologists and is very obvi-

Figure 5.2. Ungulate Exclosure, Olympic National Park

ous in two exclosures Franklin was instrumental in establishing in the South Fork of the Hoh River in 1980. In the mid-1990s Andrea Woodward and Ed Schreiner found that in these exclosures, and in others outside the park, elk influence shrub and tree recruitment by feeding preferentially on western hemlocks and western red cedars and by avoiding Sitka spruce, an unpalatable species. Exclusion of elk decreased the amount of grass and increased tree density. Shrubs inside exclosures had higher diversity and included palatable browse species such as salmonberry (*Rubus spectabilis*) and huckleberry (*Vaccinium* spp.), which had disappeared elsewhere as a result of elk preferential browsing.[45]

While as of 2009 wolves hadn't reached the Olympic Peninsula, Franklin predicts that if they return to this ecosystem, wolves will reduce elk density and impacts on understory communities. However, Franklin and Olympic National Park ecologists have an alternative perspective on the value of using cottonwoods as an indicator of these dynamics. Although the cottonwood represents an ecologically important component of riparian plant communities in general, in Olympic National Park it makes up an insignificant proportion of the hardwood community (less than 1 percent). Franklin suggests that studies based on its recruitment may be biased by failing to focus on species with greater importance in this system, such as red alder. But elk do not seem to feed much, if at all, on alder because it produces compounds that render it fairly unpalatable. This illustrates that relationships between elk and various browse species create complex community dynamics that bear further study.[46]

According to Beschta and Ripple, trophic cascades have influenced hydrology inside and outside the park. They found river channels inside the park more braided (37 percent) than outside the park (3 percent), with significantly more bare soil. They noted that these reaches historically may have been single channels, and they linked the shift to a braided condition to intense elk herbivory in riparian areas. They interpreted braiding as evidence of a degraded stream, caused by elk removing stream bank vegetation and thereby making the earth less stable alongside a river. Meanwhile, they attributed the lesser extent of braiding outside the park to human activity, such as hunting, that reduced elk herbivory on cottonwoods and bigleaf maples.[47]

Like everything else in nature, riparian ecology is complex and multicausal. Naiman suggests that while herbivory has a strong effect on stream banks by influencing plant growth and distribution, other forms of disturbance may have an equal role in shaping some of these dynamics. The biophysical processes at work in Pacific Northwest floodplain systems fundamentally shape ecological community dynamics. Debris flows, characteristic of healthy riparian systems, scour and widen streams and send big logs hurtling downriver. These events undercut stream banks, remove vegetation, and create changes in plant communities, which include succession and production of trees. Naiman proposes that the missing cottonwood age classes Beschta and Ripple observed could also have been influenced by debris flows. Additionally, Naiman and Swanson assert that braided streams are not necessarily evidence of riparian degradation. A braided river contains a network of narrow channels separated by small, temporary islands or gravel bars. Braiding occurs naturally in rivers that have a high slope and carry a large sediment load and also where rivers dramatically decrease in width as they reach floodplains, as is the case in Olympic National Park. In this park thick alder stands grow along many stream banks, helping to hold the soil in place. Naiman and his colleagues suggest that reducing large predators, especially wolves, may have resulted in significantly decreased recruitment of browsable plants that can stabilize stream banks in the Pacific Northwest; however, a braided river may not be primarily the result of this. Although it's very likely that wolves could have a strong top-down effect on this ecosystem, as elsewhere, the complexity of these interactions invites deeper inquiry.[48] Given Washington's recolonizing wolf population, we may someday have the opportunity to test these dynamics more closely.

Wind River Wolf Cascades?

At the Wind River Experimental Forest, I went for a walk in the Thornton T. Munger Research Natural Area old-growth stand with Ken Bible to examine elk herbivory. Franklin had suggested that elk, which have a high population here, have been attracted by human land use practices that create forest openings, such as timber harvesting and the abandoned tree nursery across from the cabin where I stayed. Additionally, an elk reintroduction conducted locally in the previous century, when elk numbers had reached a low point, created an unnatural situation. Nevertheless, ungulate impacts have been similar to those observed in other wolfless places, such as the upper Midwest, where intense herbivory eliminated *Trillium* from the understory.[49]

As we walked, Bible showed me abundant elk beds, tracks, and droppings that went deep into the forest, several hundred yards in from the edge. He pointed out salal (*Gaultheria shallon*), Oregon grape (*Mahonia repens*), and huckleberry pruned low to the ground and stripped of their leaves by elk. He and Franklin have installed an exclosure to begin to track the effects of herbivory here, such as changes in plant species composition. Western red cedar may provide an example of these effects. Bible explained how virtually none grew in the understory, even though this species historically had been present. Given that it is a highly palatable elk food, its absence may be related to intense herbivory. However, this pattern may soon change.[50] If the recolonizing wolf population develops at a rate similar to that in other places, such as Oregon and Montana, an ecologically effective population may become established at Wind River before long. When it does, researchers will document any changes in the forest trees and shrubs in response to a release from herbivory and other changes in this food web's dynamics.[51]

The ecological effects of wolves in Pacific Northwest rain forests may be markedly different from those in simpler systems, such as Yellowstone National Park. According to Franklin, places where concentrations of ungulates exist in this region are quite limited in spatial extent. He has found that ungulate distribution tends to reflect human settlement and activities (e.g., logging) or large and persistent natural disturbances (e.g., Mount St. Helens), which create openings in old growth that increase sprouting of tender shoots of shrubs and trees. Hence, any trophic cascades study involving wolves, elk, and plant communities should ideally consider the dominant forest landscape condition (prelogging, pre–volcanic eruption), along with the areas where we expect to see some effects of the wolf's return.

TROPHIC CASCADES in highly speciose systems are not as easy to quantify as those in simpler systems. In old-growth rain forests, as elsewhere, top-down energy combines with bottom-up effects, which include nutrient flow and disturbance. Nevertheless, trophic cascades ideas about the value of keystone predation are meaningful here. While ancient forests harbor a wealth of life, they may lack some of the highly interacting species once present, such as gomphotheres, jaguars, or wolves. We have seen how in the tropics some can be considered empty forests, with significantly altered trophic interactions. In temperate old growth, recolonizing wolves will indirectly change species assemblages as populations of trees respond to changes in herbivory, but bottom-up factors, such as disturbances (fire, floods), may interact with these effects, dampening them. Regardless of the strength or scope of keystone effects in old-growth rain forests, becoming aware of missing trophic relationships is an essential first step toward restoring ecosystems. In the next chapter we will learn more about how these relationships influence biodiversity.