FOREST ECOLOGY

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Contents

Summary

Forest ecology is the study of forest ecosystems. Forests are ecosystems in which the major ecological characteristics reflect the dominance of ecosystem conditions and processes by trees. Ecosystems are ecological systems that have the attributes of structure, function, interaction of the component parts, complexity (that reflects the structure, function and interactions) and change over time. An ecosystem can be of

almost any physical size as long as it exhibits these key characteristics, from a single plant growing in soil, to the entire world ecosystem.

The key structural components of forest ecosystems are plants, animals, microbes, soils and the atmosphere. Topography and microclimate are also important ecosystem features, but are not structural elements in the strict sense.

The key functional aspects of forest ecosystems are energy capture and biomass creation; nutrient cycling and the regulation of atmospheric and water chemistry; and important contributions to the regulation of the water cycle.

The interactions within an ecosystem involve all combinations of plant, animal and microbial interactions, interactions between organisms and the soil, and between the atmosphere and both the biotic community and the soil.

Complexity is an important attribute even though normally functioning forest ecosystems can exist at widely different levels of complexity. The importance of complexity lies in its implications for our ability to understand and predict, and therefore manage, forest ecosystems.

Forest ecosystems are continually changing. This change, initiated by external disturbance factors but largely determined by internal ecosystem processes, is vital for the maintenance of many aspects of biological diversity. In many types of forests it is essential for the long-term sustainability of the ecosystem.

"Forest stewardship" and "good, sustainable forestry" can only be defined in terms of society's desires and preferences with respect to stand and landscape-level forest conditions, functions and values. However, unless forestry is based on a respect for forest ecology and the ecological characteristics of forest ecosystems, it is very unlikely that society's long-term desires will be satisfied. Because of the long time scales of forestry, decisions about forest management must be founded on ecologically-based forecasts of ecosystem response, involving the use of ecosystem management simulation models.

1. Introduction: What is a Forest, What are Forest Ecosystems, and What is Forest Ecology?

Forests are local or regional segments of landscapes in which biological and ecological conditions and processes are dominated by the presence of trees - large, generally long-lived perennial plants characterized by a large woody stem and a large woody root system. The size and longevity of trees confer on them the ability to dominate other plant types by expropriating light and soil resources. This enables trees to control the major ecological processes, to determine the habitat for animals, microbes and other plant types, and to play a major role in determining the abundance of these other organisms in the forest. Trees also dominate the hydrological cycle, the soil development processes, the microclimate and the ecological characteristics of streams in forest ecosystems. Forests can also be dominated by large plants with woody stems that are not strictly trees, such as bamboo or tree ferns.

Ecology is the science that studies ecosystems. An ecosystem is any ecological system that exhibits five key attributes:

1. **Structure** - there are living and dead plants, animals and microbes arranged in vertical and horizontal patterns in local ecosystems and across regional landscapes. There is a physical environment that in terrestrial ecosystems consists of soil, geological substrates, and an atmosphere. In aquatic ecosystems, the medium is water, and the ecological processes may or may not be affected by sediments or geological substrates.

2. **Function** - the system of living and dead organisms, together with their abiotic environment, results in the combining of physical (light) or chemical energy with chemical elements (nutrients) from the soil, geological substrate, water or atmosphere to create the complex, high-energy, organic molecules that make up living organisms and render life as we know it possible. The energy for the creation of these molecules in forest ecosystems is provided almost entirely by photosynthesis. The chemical raw materials for their synthesis are provided by the circulation of appropriate mixtures of different nutrient elements in the ecosystem (nutrient cycling), which in turn is strongly influenced by temperature and moisture, and hence by climate, and by the action of soil animals and microbes.

3. **Complexity** Forest ecosystems are characterized by complex assemblages of different plant life forms, from lichens and bryophytes (e.g., mosses) to various types of herbs and shrubs, to climbers and trees. Associated with these different living plants is an assemblage of animals and microbes that use them as a source of energy and nutrition. Dead plant and animal matter provides the energy resource for a different set of animals and microbes that serve to decompose the organic matter and make the nutrients they contain available again for uptake by a new generation of living plants and microbes. The interactions between the living organisms, and between these organisms and both the dead organic matter and the physical environment contributes to the complexity of ecological systems.

4. **Interactions between ecosystem components**. As is the case for all systems, a key feature of an ecosystem is the interaction between the structural components. For example, soils affect plants, but plants also influence soil development. Climate determines soil and vegetation development, but plants modify local climate to produce a microclimate; vegetation can sometimes influence regional climate features and global vegetation plays a major role in global climate. Animals and microbes affect plants, but plants largely determine which animals and microbes will be affecting them.

5. **Change over time**. For humans, "nothing is as certain as death and taxes". For ecosystems, nothing is as certain as change. Just as individual animals are born, grow, mature and inevitably die, ecosystems undergo "renewal" as a result of ecosystem disturbance caused by humans or non-human processes or events. Ecosystems develop and "mature", and are eventually redisturbed and the process of renewal is repeated. This change over time is as fundamental to ecosystems as any

of their other characteristics, and in many cases is an essential requirement for their long-term stability and the maintenance of historical ranges of variation in their structure, function, complexity (including biological diversity) and the interactions of their components.

A forest ecosystem is an area of the landscape, varying in size from a local stand (a few hectares or less) to an entire continent, in which the structure, function, complexity, interactions and patterns of change over time are dominated by trees. Forest ecology is the study of these tree-dominated landscape units. Stand-level forest ecosystems are terrestrial ecosystems, but landscape-level forest ecosystems frequently include streams, rivers and lakes, and areas of non-forested terrestrial ecosystems. However, the overall character of these other types of ecosystems is strongly influenced by their location in a tree-dominated landscape.

As a science, forest ecology provides no basis for value judgements. There is no stage of forest ecosystem development, no structure, no level of function, no level of complexity and no pattern of interactions of ecosystem components that is any "better" or "worse" than any other. A young forest is no better or worse than an old forest. A forest with high productivity is no better or worse than one of low productivity. A forest with high species or structural diversity is no better and no worse than a forest with low levels of these measures of diversity. Human value systems, which have nothing to do with the science of forest ecology, provide the basis for human preferences concerning these different ecosystem attributes.

What, then, is the role of forest ecology in society? It is to describe and provide an explanation for, and an understanding of, the differences between forest ecosystems in different places, and the changes in any one forest over time. This understanding defines the range of possible social and ecological values and the environmental "services"*(environmental "services" provided by forests include regulation of the water cycle, stream flow and water quality; regulation of atmospheric* CO_2*; protection of soil and control of erosion and landslides; and provision of microclimatic shelter and the amelioration of temperature and wind.)* that a particular ecosystem can provide, and the regimes of ecosystem disturbance and recovery that are appropriate for the maintenance of a desired supply of particular values and services over time. These regimes are defined by the combination of type, frequency and severity of disturbance that will result in a non-declining pattern of change in particular types of forest ecosystem over the long term.

In this exploration of forest ecology, we will consider why forest ecosystems vary from place to place and change from time to time. This review will lead to a consideration of the ecological foundation for sustainability and stewardship: two societal goals that are based on human preferences and not on ecology, but the achievement of which requires an ecological foundation.

2. Why are Forests Different from One Part of the World to Another, at Different Locations on a Continent, and Even Locally?

The type of forest that can develop in an area is ultimately determined by climate. The broad bands of different vegetation types one can observe while traveling from sea level to the top of a tall mountain at the equator, or from sea level at the equator to sea level in the arctic, reflect changes in temperature and precipitation along these elevation/latitudinal gradients. Similarly, climatic gradients from the coast to the interior of continents, and with increasing distance away from large lakes, are associated with differences in vegetation and in the accompanying soils, animals and microbial communities. Tropical rain forest, tropical seasonal forest, tropical dry forest, subtropical forest, savanna, grasslands, evergreen warm and evergreen cool temperate forest, deciduous temperate forest, boreal forest, shrublands and tundra are major vegetation types, each of which is associated with a particular climate that determines the potential vegetation that can develop, and the associated animal and microbial communities.

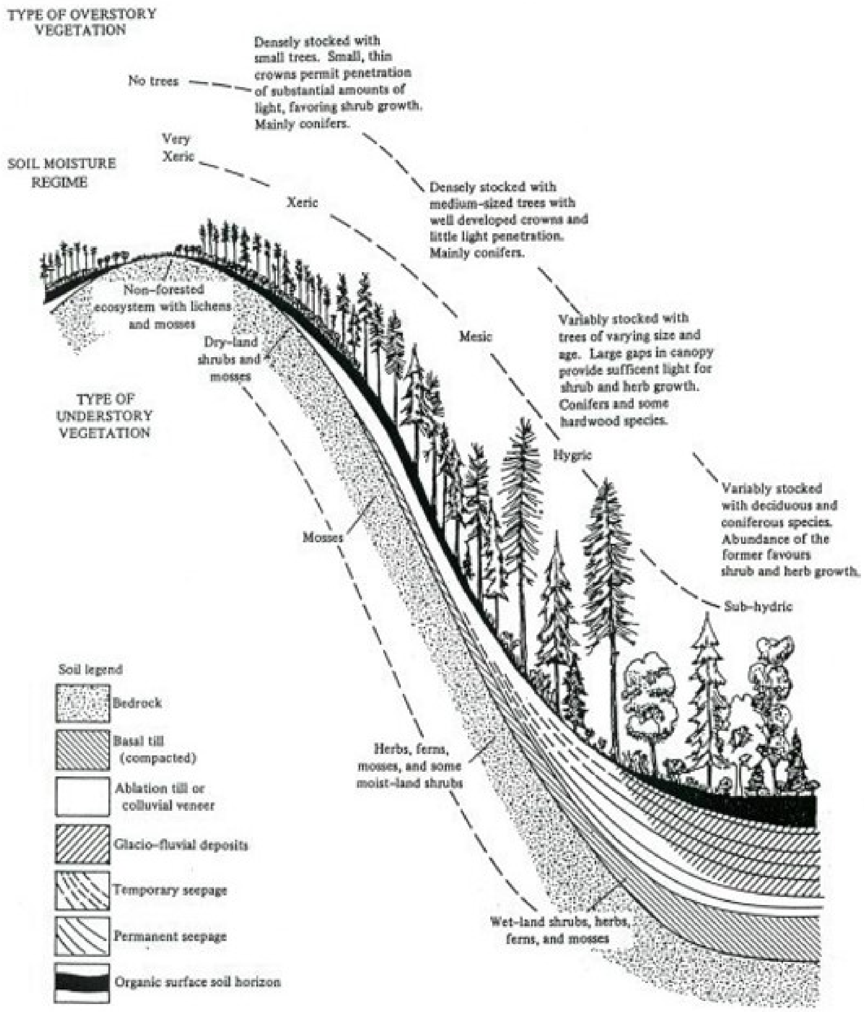

Figure 1. Variation in the structure and species composition of the plant community along a local gradient of variation in soil moisture and fertility that is associated with a local topographic gradient from the top of a small ridge to the valley below. The example is from a low elevation coastal forest in southern British Columbia.

Within a particular regional climatic area, the achievement of the climate-related vegetation potential is determined by aspect (which modifies the regional climate), the slope and the position of the ecosystem on the slope (which affects soils and soil moisture), and the soil and bedrock geology (which affects soil fertility and soil moisture). This ecological diversity (the diversity of climate, topography, geology and soil) creates both continental bands of broadly similar types of ecosystem (biomes), and local mosaics of biotic communities distributed along gradients of soil moisture and fertility, and across topographically-induced local variations in climate within the biomes. Figure 1 shows the variation in biotic communities along a local topographic gradient.

Biomes - continental-level subdivisions of the continental ecosystem - consist of life zones (defined by major climatic belts and major topographic and geological features) and plant formations (plant communities dominated by plants of a particular life form; life forms include mosses, herbs, shrubs, deciduous trees, evergreen trees, etc.). Plant formations are in turn associated with particular groupings of animals (e.g., grassland animals, tundra animals, evergreen coniferous forest animals, deciduous forest animals) and microbes.

Forest biomes are a useful level of forest classification for continental and global-level studies of major differences between forests, and of relationships between forests and global climate, but biomes are too coarse a level of subdivision for many purposes. Understanding wildlife habitat relationships, biodiversity issues, sustainable forest management and forest stewardship requires an understanding of the local mosaics of forest ecosystem types within a biome. Because biomes are based on vegetation life form, the first subdivision of forest biomes is based on the dominant tree species in mature or old forests growing on sites of average moisture and soil fertility. This defines forested ecozones or biogeoclimatic zones.

Forest biogeoclimatic zones or ecozones are a mosaic of different forest ecosystem types growing on soils of different moisture and nutrient status within a particular climatic regime or area. These different ecosystem types vary in species composition, productivity, biological diversity and response to ecosystem disturbance. They also vary in the rates and patterns of change following disturbance.

3. Why do Forests Change Over Time? The Question of Temporal Diversity

Any gardener knows that vegetation changes if left to its own devices. Within a few years of neglect, most gardens will be taken over by a variety of "weeds" - unwanted native or introduced herbs and shrubs - and within a few decades most abandoned gardens in forested areas will be colonized by young trees. It is much less obvious that mature forests change. Once a long-lived tree is large, most people fail to notice as it gets taller and develops a thicker stem. Because most forests grow and change on time scales that are a significant fraction of, or longer than, a human lifetime, many people regard unharvested forests as a permanent ecosystem condition. In reality, change is always occurring, whether this is simply because branches are dying, because individual trees are getting larger, because natural processes are causing mortality that reduces the number of living trees in an area, or because fire, wind, snow, insects, disease epidemics or forest harvesting are periodically causing major modifications to ecosystem structure, species composition and function.

Forests change over time periods of millennia or longer due to climate change. They change more frequently - perhaps every one or few centuries - because of external physical factors (such as fire, wind, snow and landslides, referred to as allogenic factors) or "external" biological factors (insect and disease epidemics, referred to as biogenic factors). In some forests, these external allogenic or biogenic disturbances may occur every few decades. Forests also change because of alterations in soil and microclimate, and in plant, animal and microbial species caused by within-ecosystem ecological processes at the population and biotic community level. This self-driven or autogenic change occurs following disturbance to the existing ecological condition caused by allogenic or biogenic disturbance processes. It is a process of ecosystem recovery back to, or towards, the pre-disturbance ecosystem condition, and is called ecological succession. Disturbance is defined as the action of allogenic and/or biogenic factors that results in rates, patterns and directions of successional change that are different from what would be expected in the ecosystem in question as a result of autogenic processes.

Changes in local and regional forest ecosystems over time are the combined result of all these processes: climate change, allogenic and biogenic change, and autogenic change. The details of the change - the degree and spatial scale of ecosystem disturbance, the rate of ecosystem recovery and the sequence of biotic communities that successively occupy and replace each other in areas that have been disturbed - are highly variable. Within any climatic area, there is an overall climatic control of the patterns and rates of autogenic recovery, but in many local ecosystems there can be a considerable range in the details, albeit within this overall control. Different temporal sequences of plant communities with different animal and microbial assemblages can occur according to the pre-disturbance forest condition, the nature and extent of the disturbance, the type of soil, and whether or not seeds or spores of particular plant species arrive in the disturbed area in time to participate in the developing plant community.

Biological diversity has become a topic of major concern around the world. The product of millions of years of evolution, biological diversity (or simply "biodiversity") is nature's "insurance policy" providing for ecosystem resilience in the face of climatic change and disturbance. It provides a vast wealth of economic and human health-related resources, and is a key part of the aesthetic, intellectual and spiritual forest values held by human society. Most people feel that the biodiversity of forests needs to be "protected" and "preserved" by minimizing ecosystem disturbance. However, the issue of biodiversity conservation is complex and requires an understanding of the origins and causes of biodiversity. These lie in:

1. Ecological diversity, most of which is unaltered and unaffected by human activity.
2. Ecosystem disturbance, which creates different ages of forest with a wide variety of different structures and plant species composition, thereby providing habitat for a wide variety of animals and microbes. Ecosystem disturbance initiates new sequences of ecological succession that create temporal diversity in the forest.

3. Autogenic ecosystem recovery (referred to as succession) which provides ever-changing soil, microclimatic and biotic conditions, ensuring that a wide variety of different species occur in any particular local ecosystem over time, and that there is a shifting mosaic of ecosystem conditions across regional landscapes that ensures a wide diversity of plant, animal and microbial habitats.

Conservation of biodiversity is thus related to appropriate types, frequencies, severities and scales of "natural" and human-caused disturbance (humans are also natural, as is the disturbance they cause), interacting with existing ecological diversity. Biodiversity objectives will only be achieved if biodiversity conservation plans are based on knowledge of how and why forest ecosystems vary from place to place, and how and why they change over time. Temporal diversity, the variation in all other measures of biodiversity over time, turns out to be the key to the maintenance of most other measures of biodiversity over longer time periods.

4. Forest Ecosystem Structure

Forest ecosystems consist of:

1. soil or some geological or organic substrate in which the trees and other plants are rooted;

2. an atmosphere and a regional climate that is modified locally by slope and aspect; a microclimate that results from the shade, the reduced wind speed and the increased humidity created by the trees; and

3. organisms, including plants. Forest ecosystem structure reflects to a great extent the horizontal and vertical arrangement of living forest plants of different life form. Life forms include mosses, liverworts and lichens; grasses and non-grass herbs (forbs); shrubs and climbers; and trees of various types, (deciduous and evergreen, coniferous (gymnosperm) and broadleaved (angiosperm), short lived and long lived, short and tall, light demanding and shade tolerant, nutrient-demanding or tolerant of poor nutrition, etc.). In addition to the living plants, there are standing dead trees (snags) in various stages of decay and collapse; dead tree stems on the ground in various stages of decomposition; and an organic layer on the soil surface (the forest floor) made up of varying combinations of dead fine roots, above ground litterfall (leaves, branches, reproductive structures), decaying wood, dead fungi, bacteria and animals, the decay-resistant faeces of soil animals, and various other types of highly decomposed organic matter. A wide variety of animals and microbes is associated with these living and dead plant components of ecosystem structure. Figure 2 shows the vertical structure of a forest stand level ecosystem.

4.3. Soil

Soil is the unconsolidated mineral material at the surface of the earth that has been so altered by physical, chemical and biological processes acting over time that it can support plant life and ecosystem processes. Some types of forest can grow in the absence of soil; some tree species, such as certain pines, have adaptations that allow them to root and grow slowly on fractured rock as long as there is adequate moisture. Others, such as alders, can fix atmospheric nitrogen, thereby enabling them to grow on chemically unweathered but physically fragmented rock material that lacks organic matter and nitrogen; they obtain the other mineral nutrients they need by creating acidity that decomposes the unweathered rock fragments, releasing the nutrients contained therein (e.g., phosphorus, calcium, magnesium, sulphur, potassium, iron and various "micronutrients"). Many trees can grow in an accumulated organic layer over rock if moisture is not limiting; acids released from the decomposing organic matter break down the rock releasing mineral nutrients. However, most trees and other plant species grow most productively on well-developed and fertile soil (a mixture of mineral and organic materials), and many can only grow in such soil.

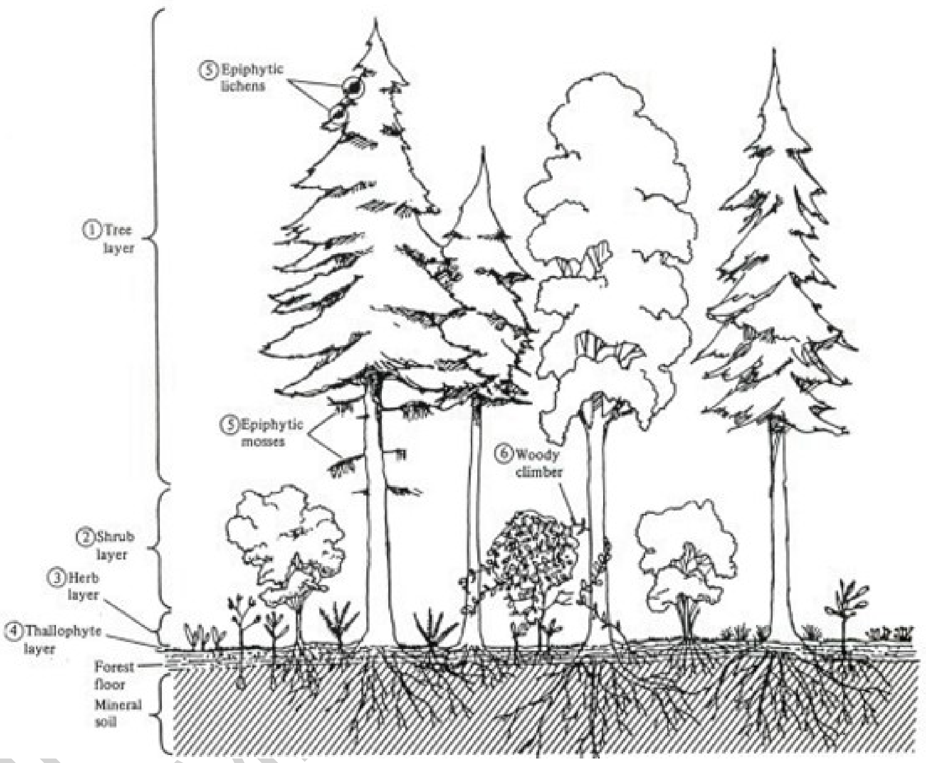

Figure 2. Plant communities have a vertical structure that reflects the life form and age of the plants, their individual growth characteristics and height growth potential, and the history of ecosystem disturbance. Both living and dead plants (not shown) contribute to the vertical structure of the forest. Variations in the vertical structure across the landscape create horizontal structure in the forest (e.g., Figure 1).

4.4. Microclimate

Forest microclimates are the altered light, radiation budgets (the balance of incoming and outgoing short and long wavelength radiation), wind speed, temperature, humidity and water balance (water inputs by rain, fog, snow and dew, and outputs by transpiration from plants and evaporation from wet plant surfaces and the soil) that are created by the trees and other forest plants below their canopies of leaves. Microclimates change dramatically when disturbance (e.g., fire, wind, logging) removes the existing canopy of leaves and the standing stems, but recovers towards pre-disturbance conditions as the leaf area of herbs, shrubs and then trees become re-established as autogenic succession takes a disturbed area back towards its pre-disturbance condition.

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Biographical Sketch

James P. (Hamish) Kimmins has been Professor of Forest Ecology, Faculty of Forestry, University of British Columbia, Vancouver, BC V6T 1Z4, since January 1969. He has a B.S. Forestry, University of Wales, 1964, an M.Sc. Forest Entomology, University of California, 1966 and a Ph.D. Forest Ecology, Yale University, 1970. He is the author of the standard textbooks "Forest Ecology" and of "Balancing Act: Environmental Issues in Forestry", and has published 77 journal papers, and 10 book chapters. He is a member of the UNESCO World Commission on the Ethics of Scientific Knowledge and Technology. He is also Director of International Programs, Forestry Faculty, UBC, and a Director of Forest Ecosystem Management Simulation Research Group, Dept. of Forest Sciences, UBC. His research interests: Forest ecosystem management, ecological role of disturbance, sustainability, ecosystem management modeling.