TEMPORAL AND SPATIAL CONTINUITY IN FOREST ECOSYSTEMS

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Summary

This chapter examines the normal course of evolution and change that forest ecosystems undergo in the absence of human influence, as well as bringing into focus the effects of some human activities. Forests, as is the case with other natural ecosystems throughout the world, do not develop spontaneously, but gradually pass through specific patterns of change of plant and animal communities. The sequential and progressive replacement of populations or community structures from simpler to more complex forms are defined "successions." The first species to colonize a new habitat at are termed "pioneer species." Although morphologically simple, the pioneers are hardy plants that can survive very unfavorable conditions; that is, they have the possibility to survive over strong external physiological and ecological constraints. Among these external constraints, intense sunlight and soils poor in nutrients are considered among the most important limiting factors, at least in tropical and equatorial climates. The process of gradual replacement by better adapted higher plants continues until a "climax" community eventually establishes, defined by ecologists as a community that remains stable providing that no natural disasters or human activities disrupts it (i.e., a community that is at a mature level in the natural ecosystem). Such mature communities tend to be self-perpetuating and long lived, as long as climate and other major environmental factors (e.g., soil conditions, drought, flood, etc.) remain essentially the same. In addition to human factors (e.g., cultivation, burning of grasslands, cutting of trees for timber and building poles, harvesting of lianas, grasses, and sedges for construction and weaving), the evolution of the various successions depends on the specific characteristics of the various soils. Thus, temperate forests are nurtured by a rich topsoil that may be as deep as 2.1 m or deeper, while the leaf mulch may exceed 31 cm in thickness. On the other hand, tropical forests have topsoils of less than 5 cm, and leaf litter is approximately 2.5 cm in depth. Stability in a system implies that there is persistence of structure over time and resilience to withstand or recover from external perturbation or stress. Stability depends on biodiversity—the number and variety of

genes, species, habitats, and ecosystems available in an area; the higher the number and variety of species, the greater the stability. All the component species are considered important for sustenance of an ecosystem's stability, irrespective of whether they are small or large in size, poisonous, ferocious, or dangerous, because each strictly occupies its own ecological niche.

1. Introduction

Forests constitute one of the major terrestrial ecosystems of the world and have fairly wide distribution both in the tropical and temperate regions. Like other ecosystems, each is an ecological unit comprising all the organisms (plant and animal communities, etc.) of the place and the nonliving or biotic components with which they interact. Ecosystems generally are not static, but dynamic.

Just as the environment is always changing due to natural or human-induced stresses, so also do the numerical abundances of the plant and animal populations fluctuate throughout time. Although ecosystems are always subject to change, they also resist disturbance and are capable of restoring themselves to their previous status. Indeed, resistance to external disturbance is a truly remarkable feature of ecosystems. This chapter examines the normal course of evolution and change that forest ecosystems undergo in the absence of human influence, as well as bringing into focus the effects of some human activities.

2. The Concept of Forest Succession

Forests, wherever they occur, certainly did not develop spontaneously, but gradually pass through specific patterns of change in plant and animal communities. Ecologists describe the sequential and progressive replacement of populations or community structure from simpler to more complex forms as "succession."

Tropical rain forest and oak–hickory forest, for instance, develop over many decades or centuries, starting with the colonization of a previously uninhabited site by a simple low-growing natural community such as lichens, mosses, or herbaceous grasses. The first species to colonize a new habitat at are termed "pioneer species." Although morphologically simple, the pioneers are hardy plants that can survive very unfavorable conditions; that is, they have the possibility to survive over strong external physiological and ecological constraints. Among these external constraints, intense sunlight and soils poor in nutrients are considered among the most important limiting factors.

Generally speaking, the pioneer species are adaptable and generalist (i.e., not specifically adapted to a given environmental situation). Therefore, they are usually called "opportunistic" species, because these so-called r-strategists have high reproductive potential for maximizing production of seeds that can be dispersed widely.

The pioneer species are usually slowly joined and gradually replaced over time by species better adapted for equilibrium high-density communities (K-strategists). The K-strategists in turn compete for their place in the next successional community. Although this situation is general in Earth's natural ecosystems, in the rain forest it may have a very rapid development, so that the various successions may change (under an external source of effects) in a limited number of years. On the mechanism of replacement of one seral community by another, most ecologists have the opinion that each stage of the successional process modifies the soil and other physical environmental factors such that the environment becomes favorable not for it, but for more advanced and better adapted forms to establish. When the next succession species arrives, it may take advantage of the favorable environment and multiply rapidly, thereby displacing the former, less adapted species. Characteristically, such stage or sere is dominated by a single species.

The process of gradual replacement by better adapted higher plants continues until a "climax" community eventually establishes, defined by ecologists as a community that remains stable providing that no natural disasters or human activities disrupts it (i.e., a community that is at a mature level in the natural ecosystem). Such mature communities tend to be self-perpetuating and long lived, as long as climate and other major environmental factors (e.g., soil conditions, drought, flood, etc.) remain essentially the same. Although in the common sense a forest at a climax stage is an ancient and undisturbed patch of wooded territory, it is evident that fundamental differences occur in the evolution of the various forest successions in temperate versus tropical regions. In fact, in addition to human factors (e.g., cultivation, burning of grasslands, cutting of trees for timber and building poles, harvesting of lianas, grasses, and sedges for construction and weaving), the evolution of the various successions depends on the specific characteristics of the various soils. Thus, temperate forests are nurtured by a rich topsoil that may be as deep as 2.1 m or deeper, while the leaf mulch may exceed 31 cm in thickness. On the other hand, tropical forests have topsoils of less than 5 cm, and leaf litter is approximately 2.5 cm in depth. Typically, below the soil horizon lies a red lateritic clay. In general, tropical forest soils are so thin that nutrient stocks must be held in the biomass, whereas in temperate forests a much higher proportion of the stock is held in the soil. In practice, in the tropical forests the nutrient reservoir is in the plants themselves, with a very complicated network of surface roots retrieving the nutrients released from plant and animal remains by termites, fungi, and other decomposers.

The succession of plant forms (and the animals they harbor) is so regular and predictable that ecological succession was at one time viewed as analogous to the developmental process of a single organism, with each stage making way for the next by "preparing" the soil and other environmental factors. Now, any ecological succession is viewed rather as the outcome of a series of contests, such as that between mono-layered and multilayered trees.

Towards the end of the twentieth century, a large volume of literature accumulated, throwing more light onto the consequences of succession in forests from immature to mature stages. A model of forest succession (Table 1), known today amongst ecologists and foresters, indicates that the early stages of succession are characterized by relatively few species, low biomass, and a largely extrabiotic source of nutrients. The ratio between gross production and biomass is usually high, and the production is greater than respiration ($P > R$). Furthermore, energy is channeled through relatively few pathways to many individuals of a few species, and production per unit is high. The food chains are typically short and linear, largely of the grazing type. The mature stages, on the other hand< are characterized by many species (e.g., perennial herbs and trees), high biomass, and a nutrient source largely organic in nature. Although production may be high, the ration between gross production and biomass is lowered, and production equals respiration ($P = R$). Energy is channeled down many diverse pathways and shared by many species. Food chains become increasingly complex and largely detrital. As the forest develops from immature to mature stages, both stratification and diversity increase and niches change from broad and general to narrow and specialized.

Characteristic	Developing/immature ecosystem	Resultant mature ecosystem
Food chain	linear	interlinked
Total organic matter	low	high
Nutrients	freely available	incorporated
Species diversity	low	high
Habitat/range of organisms	large/general	small/specialised
Nutrient cycle	open	closed
Speed of exchange with the environment	rapid	slow
Symbiosis, parabiosis	undeveloped	developed
Nutrient storage	low	high
Entropy (unavailable energy)	high	low
Elasticity (flexibility)	high	low
Productivity	high	low
Sustainability (stability)	poor	good

Table 1. Some characteristics of two types of forest ecosystem, according to a popular mathematical model of ecological successions
(Adapted from Arndt (1981).)

Both the increased diversity of species and the increased number of niches are deemed to be the product of stratification.

Ecologists recognize two types of succession, namely primary and secondary succession. Both categories may be applied to forest ecosystems, and are convenient concepts to introduce. Primary succession refers to the sequential replacement of populations in an area that has not previously been colonized by any community, such as bare rock or a sand dune. Because no life had established there before, the transformation of such a barren environment until a climax community establishes typically takes between hundreds and a thousand years. Although not directly linked with forest ecosystems, a graphic example of primary succession is represented by the Galapagos Islands, where relatively new islands were created by volcanic eruptions about 2.5 million years ago. With time, the volcanic rock was weathered into fine or tiny mineral particles by rainfall. The first life forms to reach these islands were marine organisms and sea birds, particularly the "guanos." The droppings of these guanos provided a suitable habitat for bacterial spores conveyed by the wind. As time passed,

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Biographical Sketch

Dr. Luca Luiselli obtained the degree of Doctor in Natural Sciences at the University of Rome "La Sapienza" with a thesis on the comparative eco-ethology of some populations of Italian vipers. Since 1996 he has been a research associate with several industry organizations of the Ente Nazionale Idrocarburi group in Nigeria, as well as with conservation organizations in both Africa and Italy, including several national parks. He has been working for the environmental departments of several oil companies, conservation organizations (e.g., Cercopan), and in cooperation with scientists based at the Rivers State University in Nigeria. He is also a researcher associated with the National Park of Gran Sasso-Laga, the National Park of Majella, the Abruzzi National Park, and the Duchessa Mountains Natural Park. He is chairman for Nigeria of the International Union for Conservation of Nature–Species Survival Commission (IUCN/SSC) for DAPTF, a member of the IUCN/SSC TFTSG, and has won seven international scientific research prizes (four by Chelonian Research Foundation, two by Conservation

International and one by IUCN/SSC Declining Amphibian Populations Task Force (DAPTF)). He is also coeditor of *Amphibia-Reptilia,* associate editor of *Endangered Species Research,* and serves on the advisory editorial board of *Herpetozoa, African Journal of Herpetology, Chelonian Conservation and Biology, Applied Herpetology*. In the last 15 years, he has published over 150 papers in peer-reviewed journals, including high impact periodicals (e.g., Nature, Oikos, Oecologia, etc). His main research interests are on the ecology of snakes in tropical and temperate regions, and on the modeling of forest reptile communities in areas under strong environmental stress.