ECOSYSTEM DEVELOPMENT

The process of ecological succession is fundamental to the development of any ecosystem. Such succession consists of three basic patterns. It is an orderly process of community development that is reasonably directional and predictable and results from the modification of the physical environment by the biological community that is present. The physical environment determines the pattern and the rate of change, and often limits succession. This process culminates in a stable ecosystem in which the maximum biomass and symbiotic function between the organisms is maintained per unit of available energy flow. Genetic changes involving organisms are expected to accompany any successional gradient from simple to complex because quantity production characterizes young and almost linear ecosystems, while quality production and feedback mechanisms characterize mature ecosystems through intricate matrices. In food production by humans, the trend is often to focus on simple linear ecosystems with their inherent susceptibility to catastrophic events such as drought in southern Africa and elsewhere.

In more simple ecosystems, such as the Namib Desert and the south-western Kalahari, or those that are in the early stages of succession, such as after deforestation or overgrazing, the rate of primary production or energy fixation, sometimes referred to as the total photosynthesis, exceeds the rate of respiration by a community or the cost of energy maintenance. This is reversed in mature ecosystems where energy flow becomes maximal and energy fixation is small. As ecosystems such as grasslands, savannas and evergreen forests mature, they develop a matrix of food chains that link into feedback
systems to become a *food-web*. In the southern African savannas, for example, this consists of a mix of grasslands and woodlands as the primary producers, small and large herbivores, small and large predators and ultimately a multitude of decomposers such as beetles and bacteria. In young ecosystems, such as bare soil that is being reclaimed vegetationally, that are in the early stage of succession these food chains are linear and relatively simple and usually consist of grazing food chains that form simple plant-herbivore-carnivore sequences. As ecosystems mature, the food chains become more complex and form webs with the bulk of the biological energy flow following detritus pathways. For example, in a mature forest less than 10 per cent of the annual net production of energy is consumed by herbivores in a living state while most of it is utilized as detritus (dead matter) by interactions between animals and microorganisms. Uninterrupted succession creates increasingly more intimate associations and reciprocal adaptations between plants and animals. The plants reduce their exposure to herbivory by developing indigestible tissues such as cellulose and lignin. The ecosystem gradually creates feedback mechanisms between plants and herbivores and increases predator pressure on the herbivores. Such food-web matrices allow the maintenance of a large and complex organic structure and mitigate disturbances that are caused by the physical environment. However, these protective mechanisms can still be overcome by irruptive environmental events such as fire, floods or drought that cause undue stress in ecosystems.

![Namib Desert, Dubis, Kaokoland, Namibia - August 1981](image)

The development and maintenance of species diversity in ecosystems through an increase in the variety of species and the reduced dominance of a specific species, or small groups of species, is a general probability during succession towards ecosystem maturity. This trend is opposed to some degree by an increase in the size of the organisms that are present, an increase in the length and complexity of life histories, and an increase in interspecific competition which may culminate in the competitive exclusion of some species. This would reduce diversity in the most mature ecosystems. Whether or not species diversity continues to increase during succession depends on whether the increase in potential ecological niches that result from increased biomass, stratification and other consequences of increasing biological...
organization exceed the effects of increasing size and competition. A niche is the ecological role of a specific type of organism in an ecosystem.

As succession continues and ecosystems mature there will be an increase in the closure of the biogeochemical cycle of the major nutrients such as nitrogen, phosphorus and calcium. Mature ecosystems therefore have a greater capacity than young ones to entrap and retain nutrients for cycling within the ecosystem. For example, in the Northern Temperate watersheds of America it has been estimated that only 8 kg/ha of the total 365 kg/ha of exchangeable calcium is being lost to stream outflow in a mature forest. Of the calcium that is being lost, 3 kg/ha is being replaced by rainfall to leave 5 kg/ha to be replaced by weathering of the underlying rock formations. Reducing the size of a forest creates increasing losses of nutrients through stream outflow. In turn this may cause increasing eutrophication problems downstream. This problem is especially relevant in the high-rainfall tropical and subtropical, where most of the nutrients in the evergreen forests are tied up in the biomass with less in the soil. The loss of such a forest can therefore have an irreversible effect on biomass production. Moreover, young ecosystems are characterized by high primary production of energy (photosynthesis) as opposed to mature ecosystems where the production is lower but of better quality.

The overall strategy of ecosystem development through continual succession is to achieve as large and diverse an organic structure as is possible within the limits that are set by the available input of energy and the prevailing physical conditions. Mature ecosystems also develop important symbiotic partnerships such as mutualism, predation, parasitism and commensalism which involve non-related organisms. The biotic control of herbivory, population density and nutrient cycling in many cases provide the major positive-feedback mechanisms that contribute to the stability of mature ecosystems by preventing destructive oscillations. The mute question remains whether mature ecosystems age and have a limited expectation of life.
Resilience is a feature of a mature ecosystem which allows it to return to its function following a severe but irregular perturbation such as a major drought, flood or fire. When such a perturbation becomes a regular event, an ecosystem may be maintained at an intermediate stage of development which can eventually lead to its demise. In wetlands the recurrent changes in water levels that are caused by seasonal flooding, however, are the basis for ecosystem maintenance. Periodic fires play a similar role in the maintenance of savannas while regular fires keep the Serengeti Plains in their grassland mode. This phenomenon is also known as pulse stability. If humans are to survive in a world with an increasing human population the answer seems to lie in the maintenance of ecosystems that balance youth and maturity. The role of herbivores and carnivores in maintaining ecosystem functioning will be dealt with in Sections 8.1.9.1, 8.1.9.2 and 8.1.9.3.

Serengeti Plains, Serengeti National Park, Tanzania - July 1996