

## Succession and Ecosystems

**A** Ecologists use the term "succession" to refer to the changes that happen in plant communities and ecosystems over time. In the early twentieth century, the American ecologist Frederic Clements pointed out that a succession of plant communities would develop after a disturbance such as a volcanic eruption, heavy flood, or forest fire. An abandoned field, for instance, will be invaded successively by herbaceous plants, shrubs, and trees, eventually becoming a forest.

**B** The first community in a succession is called a pioneer community, while the established community at the end of a succession is called a climax community. Pioneer and successional plant communities are said to change over periods of 1 to 500 years. These changes—in plant numbers and the mix of species are cumulative. Climax communities themselves change but over periods of time greater than about 500 years. The final stage of a succession is not predictable or of uniform composition. There is usually a good deal of turnover in species composition, even in a mature community. The nature of the climax community is influenced by the same factors that influence succession. Nevertheless, mature natural environments are usually in equilibrium. They change relatively little through time unless the environment itself changes. Clements and other early ecologists saw an almost lawlike regularity in the order of succession, but that has not been substantiated. A general trend can be recognized, but the details are usually unpredictable. Succession is influenced by many factors: the nature of the soil, exposure to sun and wind, regularity of precipitation, chance colonizations, and many other arbitrary processes.

**C** For Clements, the climax community was a "superorganism," an organic entity. Even some authors who accepted the climax community concept rejected Clements' characterization of it as a superorganism, and it is indeed a misleading metaphor. An ant colony may be legitimately called a superorganism because its communication system is so highly organized that the colony always works as a whole and appropriately according to the circumstances. But there is no evidence for such an interacting communicative network in a climax plant formation. Many authors prefer the term "association" to the term "community" in order to stress the looseness of the interaction.

**D** Even less fortunate was the extension of this type of thinking to include animals as well as plants. This resulted in the "biome," a combination of coexisting flora and fauna. Though it is true that many animals are strictly associated with certain plants, it is misleading to speak of a "spruce-moose biome," for example, because there is no internal cohesion to their association as it would be with an organism. The spruce community is not substantially affected by either the presence or absence of moose. Indeed, there are vast areas of spruce forest without moose. The opposition to the Clementsian concept of plant ecology was initiated by Herbert Gleason, soon joined by various other ecologists. Their major point was that the distribution of a given species was controlled by the habitat requirements of that species and that therefore the vegetation types were a simple consequence of the ecologies of individual plant species.

**E** With "climax," "biome," "superorganism," and various other technical terms for the association of animals and plants at a given locality being criticized, the term "ecosystem" was more and more widely adopted for the whole system of associated organisms together with the physical factors of their environment. Eventually, the energy-transforming role of such a system was emphasized. An ecologist is concerned primarily with the quantities of matter and energy that pass through a given ecosystem, and with the rates at which they do so. Today one speaks of the ecosystem when referring to a local association of animals and plants, usually without paying much attention to these energy aspects.

**F** At one time, ecologists believed that species diversity made ecosystems stable. They believed that the greater the diversity the more stable the ecosystem. Support for this idea came from the observation that long-lasting climax communities usually have more complex food webs and more species diversity than pioneer communities. Ecologists concluded that the apparent stability of climax ecosystems depended on their complexity. To take an extreme example, farmlands dominated by a single crop are so unstable that one year of bad weather or the invasion of a single pest can destroy the entire crop. In contrast, a complex climax community, such as a temperate forest, will tolerate considerable damage from weather to pests.

**G** The question of ecosystem stability is complicated, however. Stability can be defined as simply lack of change. In that case, the climax community would be considered the most stable, since, by definition, it changes the least over time. Alternatively, stability can be defined as the speed with which an ecosystem returns to a particular form following a major disturbance, such as a fire. This kind of stability is also called resilience. In that case, climax communities would be the most fragile and the least stable, since they can require hundreds of years to return to the climax state.

**H** Even the kind of stability which is defined as simple lack of change is not always associated with maximum diversity. At least in temperate zones, maximum diversity is often found in mid-successional stages, not in the climax community. Once a redwood forest matures, for example, the kinds of species and the number of individuals growing on the forest floor are reduced. In general, diversity, by itself, does not ensure stability. Mathematical models of ecosystems likewise suggest that diversity does not guarantee ecosystem stability—just the opposite, in fact.

**I** Many ecologists now think that the relative long-term stability of climax communities comes not from diversity but from the "patchiness" of the environment, an environment that varies from place to place supports more kinds of organisms than an environment that is uniform. A local population that goes extinct is quickly replaced by immigrants from an adjacent community. Even if the new population is of a different species, it can approximately fill the niche vacated by the extinct population and keep the food web intact.

**Questions 15-20:** The reading passage has nine paragraphs labelled **A-I**. Which paragraph contains the following information?

**NB** You may use any letter more than once.

15. An opposition to the idea of plants and animals being associated with "superorganisms" \_\_\_\_\_
16. Examples of various ecosystems which demonstrate that the degree of species diversity results in a stable ecosystem. \_\_\_\_\_
17. A discussion of random processes affecting specific details of successions. \_\_\_\_\_
18. Disagreements over the meaning of an ecology term intended to identify the most stable ecosystem. \_\_\_\_\_
19. Mention of a new type of environment that is thought to increase stability by supporting a wide variety of organisms. \_\_\_\_\_
20. A reference to a new term that gradually replaced discredited terms for the combination of a physical environment and the plants and animals which live together there. \_\_\_\_\_