

Chapter 5: Evolution of biocenoses

5.1 Concept of succession

Ecological succession is the natural process of evolution and development of an ecosystem through a sequence of stages, from the initial recolonization to a theoretical climactic stage. The type of succession depends on the nature of the ecological disturbance that triggered the change, such as clearing, logging, fire, or grazing by domestic animals.

Ecological succession can thus be viewed as a theoretical sequence of steps describing, in time and space, the complete evolutionary cycle of a given ecological area. As an evolutionary consequence of competition, succession can be evaluated from the perspective of ecosystem ecology, considering both the species composition and the spatial structure of the community.

This process corresponds to a succession of habitats and living communities (biocenoses). The term “succession” refers to the temporal sequences, which may be linear or cyclic, observed in ecosystems. These sequences primarily involve living communities, which are the most visible indicators of change. However, they also affect physical and chemical factors of the habitat (biotope). Changes in these abiotic factors may result from modifications in communities, or conversely, changes in the physicochemical parameters may drive alterations in biocenoses.

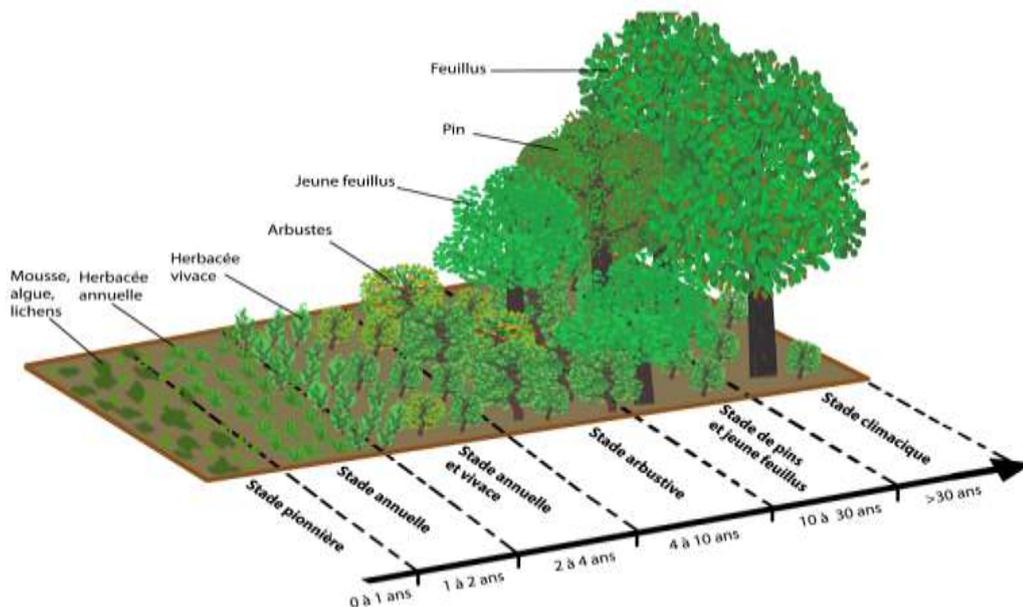


Figure 5.1. Theoretical schematic of ecological succession over time. Adapted from Dupuis-Tate & Fischesser (2017).

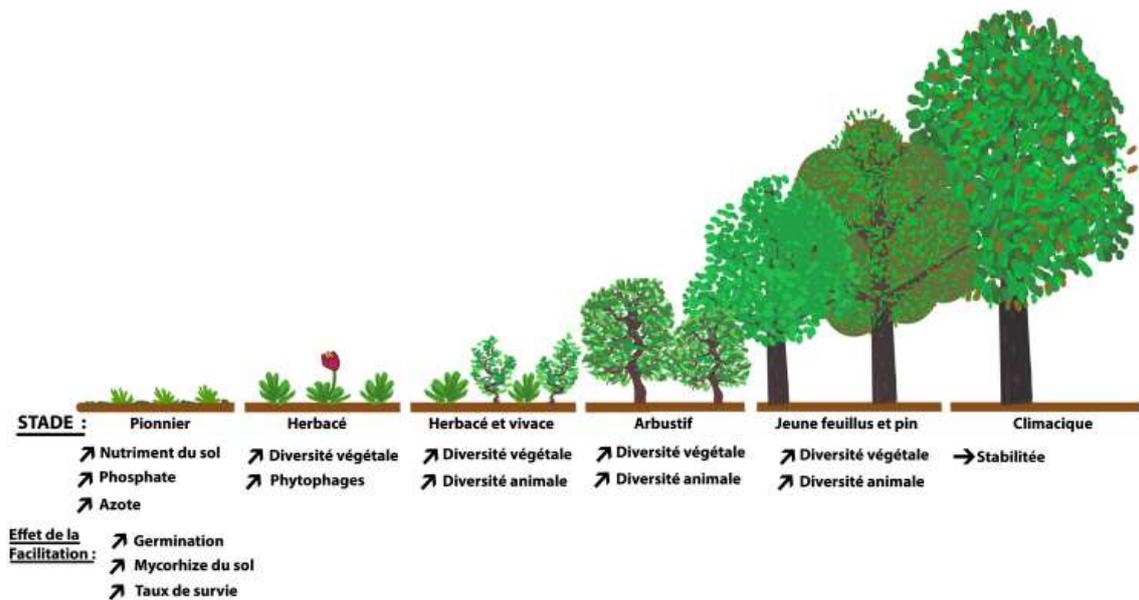


Figure 5.2. Summary of general effects and facilitation on the stages of theoretical ecological succession. Adapted from Chapin et al. (1994).

5.1.1 Autogenic Succession

Autogenic succession occurs when a linear or cyclic succession is spontaneously driven by the community itself, rather than by changes in the abiotic conditions of the habitat. In other words, the community actively modifies its environment, leading to changes in species composition over time.

Examples of autogenic succession include:

- grassland communities progressing naturally into a climax forest;
- decomposition of a dead tree trunk, on which animal assemblages (synusiae) successively colonize.

In autogenic succession, each stage of the community contributes to creating conditions that favor the next stage, without external forcing.

5.1.2 Allogenic succession

Allogenic succession refers to successions driven by gradual or abrupt changes in the abiotic environment, rather than by the biological activity of the community.

Examples of allogenic succession include:

- Post-glacial successions, where environmental conditions changed over millennia ;
- Conversion of a climax forest into cultivated land;
- Changes in the herbaceous layer under a forest canopy as the canopy becomes denser.

A stage in succession refers to a distinct step in the sequence.

- Pioneer stages are unstable and transient, often colonized by opportunistic species;
- Climactic or paraclimactic stages are stable or stabilized by external constraints (e.g., human intervention), representing the terminal state of the succession.

5.1.3 Cyclical succession

Cyclical succession is relatively rare. In such successions, regardless of the disturbance, the ecosystem returns to the climax state.

In cyclical succession :

- Regeneration refers to the phase in which the ecosystem progresses from the pioneer stage to the terminal stage;
- The final stage is always climactic or paraclimactic, until a disturbance resets the system back to the pioneer stage.

Example: The mesophilic heathlands of Brittany illustrate this process. In aged stages, either the accumulation of undecomposed organic matter may ignite due to self-heating from fermentation or external causes (accidental or intentional fire). The heathland is then destroyed and regenerates either from pyrophilous plant seeds, whose dormancy is broken by fire, or through coppice regrowth.

5.1.3 Cyclical succession

Cyclical successions are relatively rare. In this type of succession, regardless of the disturbance, the ecosystem ultimately returns to the climax stage.

In cyclical succession :

- the term regeneration refers to the phase during which the ecosystem progresses from the pioneer stage to the terminal stage.

- there is always a final stage, either climactic or paraclimactic, which persists until a disturbance resets the system from the terminal stage back to the pioneer stage.

Example: The mesophilic heathlands of Brittany provide a clear illustration. In older stages, the accumulation of undecomposed dry matter may ignite either due to self-heating from fermentation or external causes (accidental or intentional fires), resulting in complete destruction of the vegetation. The heathland then regenerates either:

- from pyrophilous plant seeds, whose dormancy is broken by the passage of fire;
- or through coppice regrowth from surviving stumps.

This example highlights how cyclical succession maintains ecosystem dynamics and resets ecological stages after disturbances, ensuring the long-term persistence of the ecosystem.

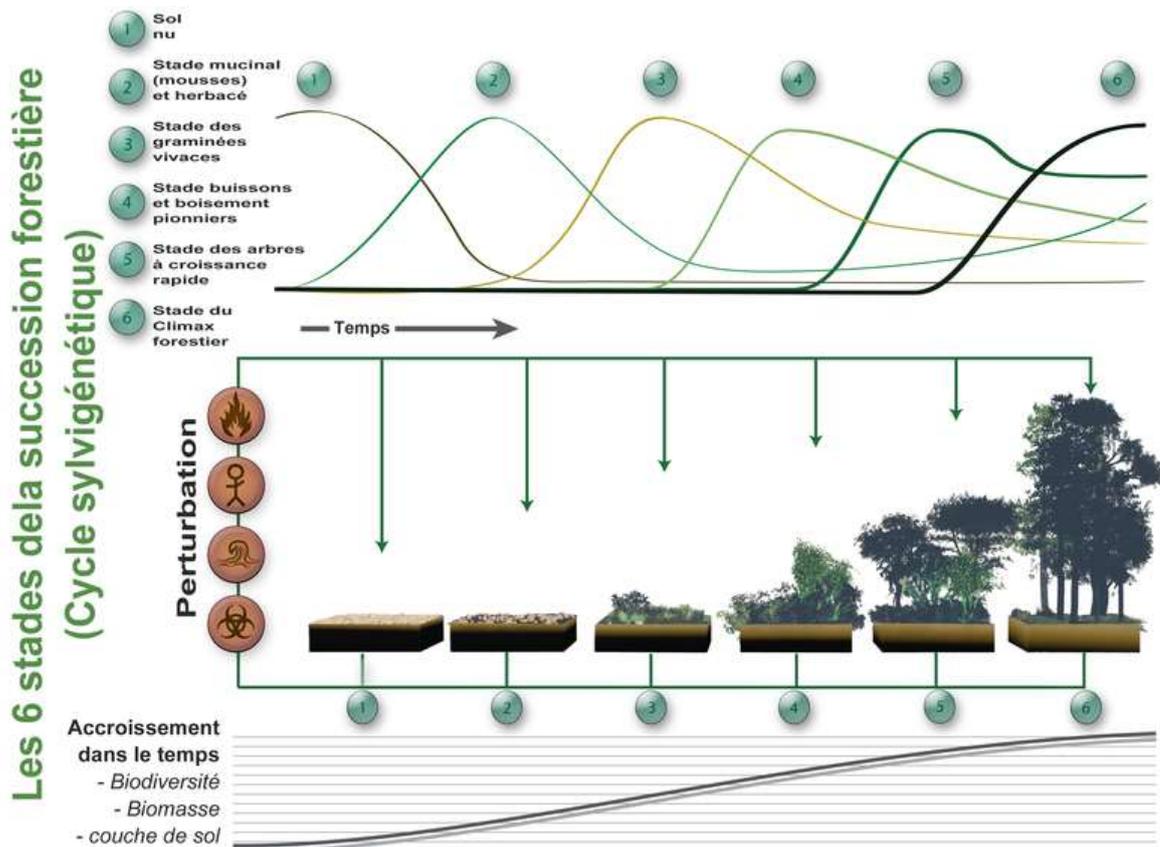


Figure 5.3. Example of a cyclical succession in a forest ecosystem. Adapted from Dupuis-Tate & Fischesser (2017)

5.1.4 Primary succession

Primary succession refers to the long-term ecological process by which living communities establish and develop on a previously uncolonized substrate, or on a substrate, that has lost all biological legacy (soil, seeds, propagules). This type of succession is typically slow, as it begins under extreme abiotic conditions and requires progressive modification of the environment by pioneer organisms.

Primary succession can be classified into two contrasting dynamics:

a) Progressive primary succession

Progressive primary succession occurs when biological communities successively replace one another, leading to increasing structural complexity, species diversity, biomass, and soil development, ultimately reaching a relatively stable climax stage.

This process generally begins with pioneer species (lichens, mosses, microorganisms), which are capable of colonizing bare substrates such as volcanic rocks, glacial moraines, sand dunes, or newly exposed soils. These organisms contribute to:

- physical and chemical weathering of the substrate;
- accumulation of organic matter ;
- gradual formation of soil, thereby facilitating the establishment of herbaceous plants, shrubs, and eventually trees.

Progressive primary succession is often associated with the facilitation model, in which early colonizers modify environmental conditions in ways that favor later species.

b) Regressive primary succession

Regressive primary succession occurs when disturbances cause an ecosystem to shift from a climax or advanced stage toward less developed stages, potentially reverting to pioneer conditions. These disturbances may be:

- natural (volcanic eruptions, landslides, severe fires) ;
- or anthropogenic (deforestation, mining, intensive land use).

In such cases, the structure and functioning of the ecosystem are simplified, biodiversity decreases, and soil characteristics may deteriorate. If disturbances persist or intensify, the ecosystem may be prevented from returning to the climax state, leading to degraded or paraclimactic systems.

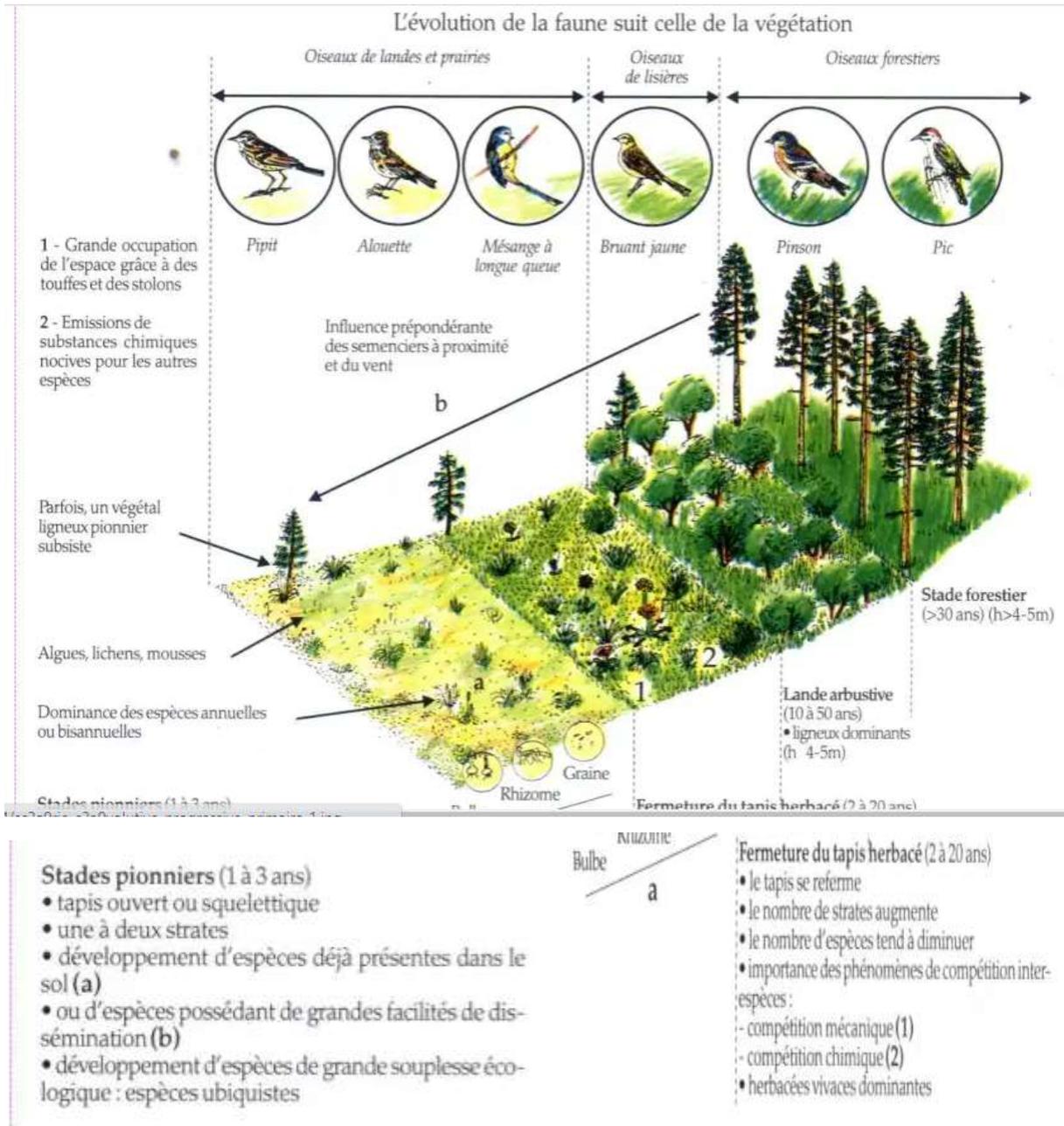


Figure 5.4. Exemple de succession progressive primaire

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5.1.5 Secondary succession

Secondary succession refers to the evolution of biological communities in an environment that was previously occupied by a biocenosis but has undergone a disturbance that did not destroy the soil or all forms of life (seed bank, roots, microorganisms). Unlike primary succession, the substrate remains biologically active, which generally makes the process of recolonization faster.

Secondary succession may be described as progressive or regressive when the final stage of succession necessarily corresponds to a paraclimax, rather than to the natural theoretical climax.

The paraclimax refers to a persistent vegetation formation composed of species that do not correspond to the potential climax of the environment. It results from anthropogenic disturbances such as land clearing, overgrazing, repeated fires, agriculture, or urbanization. It therefore represents a mature stage stabilized by an external constraint, most often of human origin.

In many cases, the paraclimactic final stage becomes unavoidable, because disturbances lead to irreversible modifications of soil conditions (soil erosion, nutrient depletion, compaction, salinization), which prevent the ecosystem from returning to its natural climax.

Example:

A classic example is provided by Mediterranean garrigue and maquis, which have replaced the original Mediterranean forest (oak forests and evergreen woodlands). As a result of centuries of deforestation, repeated fires, and pastoral pressure, these paraclimactic formations have become stabilized, and it is now highly unlikely to observe the re-establishment of the original primary forest in these regions.

Moreover, in the current context of global climate change, it is likely that new paraclimax states will develop in many ecosystems, sometimes over much shorter timescales than previously expected. Changes in temperature regimes, precipitation patterns, and disturbance frequencies (droughts, fires, storms) may accelerate these dynamics and lead to the long-term establishment of new communities that differ markedly from the historical climax.

In summary:

- the climax results from the natural dynamics of the environment;
- the paraclimax is the product of stabilization under external constraints, most often anthropogenic.

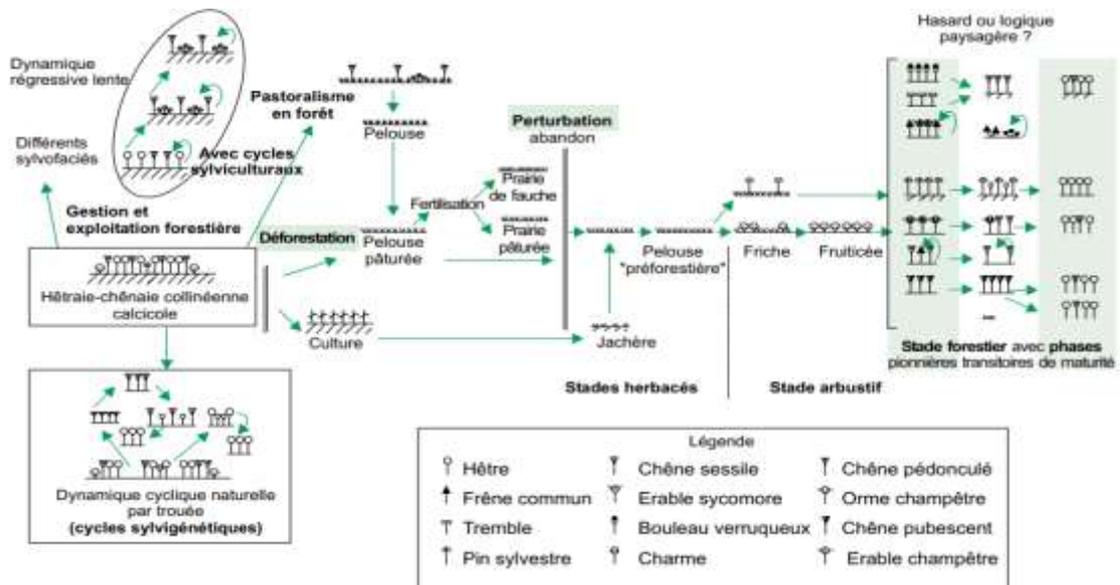


Figure 5.5. Example of progressive secondary succession (external linear dynamics) (after Jean-Claude Rameau, 1999).



Figure 5.6. Forêt mixte climacique représente la phase finale de la succession écologique, dans laquelle la structure et la composition floristique de la végétation restent relativement stables dans le temps » (Odum, 1969).

5.1.6 Anthropogenic succession

Anthropogenic succession refers to the sequence of evolutionary stages, most often involving degradation, observed within an ecosystem as a direct or indirect result of human activities. These successions mainly arise from modes of land use and resource exploitation (intensive agriculture, deforestation, overgrazing, urbanization, mining activities, repeated fires), which profoundly alter the structure and functioning of ecosystems.

In most cases, anthropogenic successions are regressive in nature, leading to a simplification of biological communities, a reduction in biodiversity, a loss of biomass, and the progressive degradation of soils. Anthropogenic disturbances can disrupt natural regeneration mechanisms and prevent ecosystems from returning to more complex and mature stages.

When regeneration becomes possible, either deliberately through ecological restoration or spontaneously following the cessation of pressures, it rarely results in the re-establishment of the natural climax. More often, the ecosystem evolves toward a paraclimax, more or less degraded, stabilized by the legacy effects of past disturbances (soil nutrient depletion, erosion, altered hydrological regimes, loss of the seed bank).

The process of desertification represents the most extreme and alarming example of anthropogenic succession. It results from the combined action of anthropogenic factors (soil overexploitation, deforestation, overgrazing) and climatic factors (recurrent droughts, global warming), leading to irreversible land degradation, loss of biological productivity, and the long-term establishment of near-desert landscapes.

Unfortunately, desertification processes are accelerating worldwide, particularly in arid and semi-arid regions. This highlights the critical importance of sustainable ecosystem management, conservation policies, and ecological restoration strategies in order to limit the extent and irreversibility of anthropogenic successions.

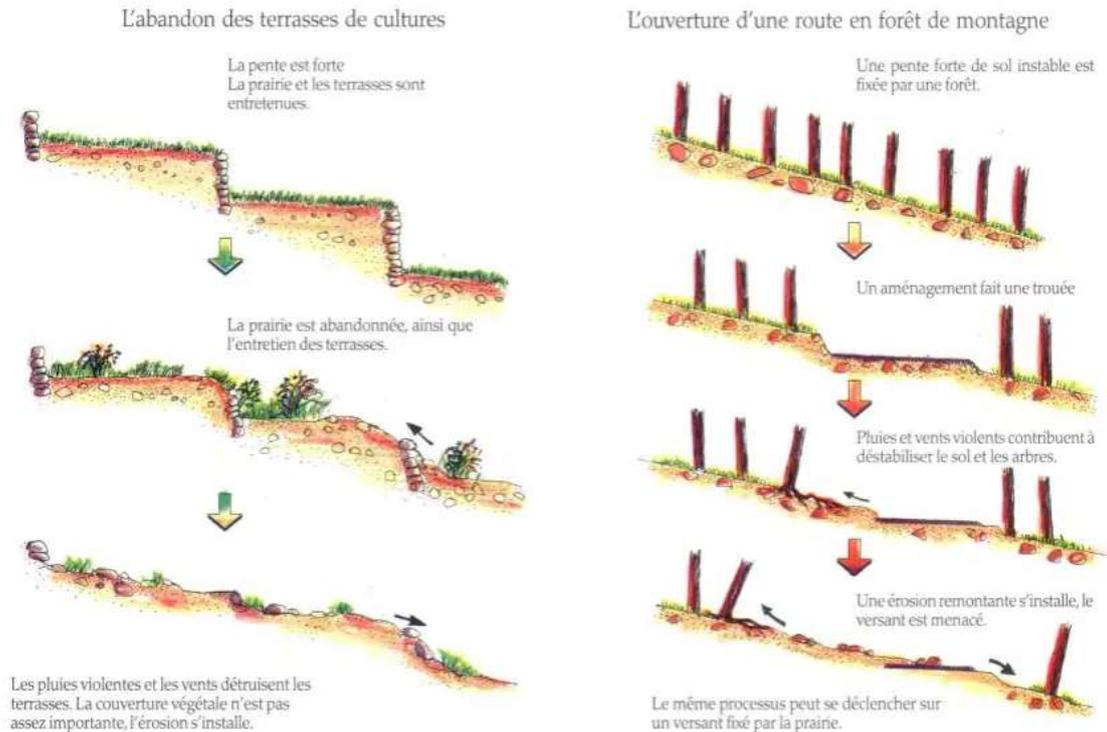


Figure 5.7. Exemple de succession régressive

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5.2 Concept of the climax

In ecology, the climax refers to a theoretical state of dynamic equilibrium reached by a biological community, particularly a plant community, when it is in stable and long-lasting harmony with the edaphic (soil) and climatic factors of its environment. This state corresponds to the ultimate stage of ecological succession, toward which an ecosystem naturally tends in the absence of major disturbances.

The climax is not a static or fixed condition, but rather a dynamic equilibrium, characterized by natural fluctuations in populations and ecological processes, while maintaining a globally stable structure. It reflects an optimal adaptation of species to local environmental conditions and an efficient functional organization of the ecosystem.

Any disturbance, whether natural (fires, storms, floods, volcanic eruptions) or anthropogenic (land clearing, agriculture, urbanization, overexploitation of resources), leads to the destruction or destabilization of the climactic state. Such disturbances cause the ecosystem to revert to earlier stages of succession.

However, in the absence of further disturbances, both the soil and the plant community are capable of evolving once again toward the climax through processes of regeneration and ecological succession. This tendency to return to equilibrium reflects the resilience of the ecosystem.

Thus, the climax represents a state of equilibrium toward which the ecosystem tends. The ability of an ecosystem to resist disturbances and to maintain its functional organization is referred to as ecological homeostasis. The higher the degree of homeostasis, the greater the ecosystem's capacity to absorb disturbances without undergoing profound changes in its structure and functioning.

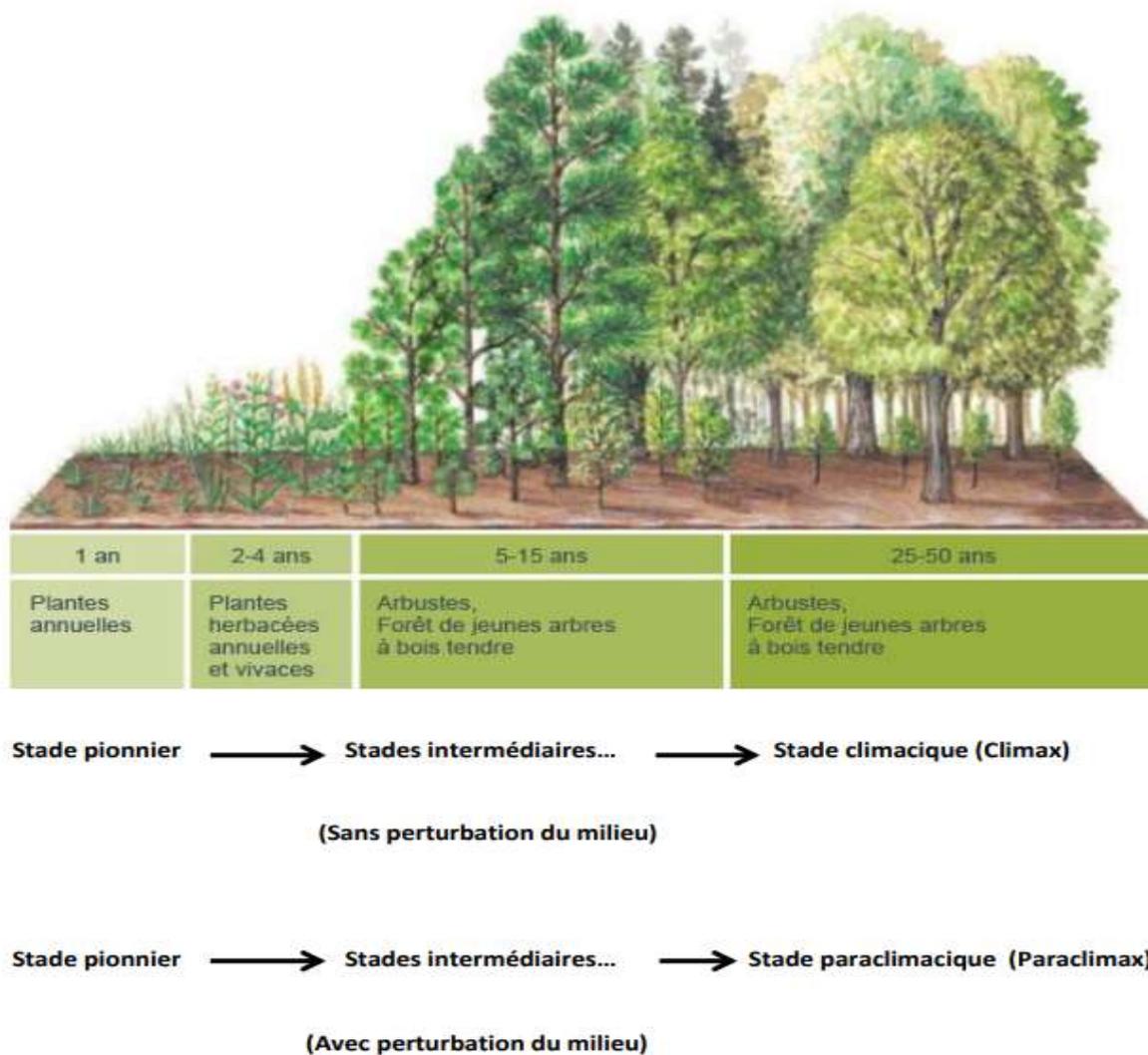


Figure 5.8. Illustration schématique de la succession écologique progressive, depuis les plantes annuelles jusqu'à une forêt jeune, selon le modèle classique de la succession végétale (Odum, 1969).

5.3 Concept of ecotone

An ecotone (biogeographical zone, edge, or boundary) is an ecological transition zone between two or more ecosystems.

For example, an estuarine zone constitutes an ecotone between the marine ecosystem, the river (fluvial) ecosystem, and the terrestrial ecosystem.

The progressive or irregular variation of hydrological, pedological, and thermal parameters at the boundaries between adjacent ecosystems creates a mosaic of habitats, resulting in the interpenetration of the fauna and flora of these ecosystems. Ecotones therefore host species and communities from the neighboring environments, as well as distinct communities that are specific to the ecotone itself.

These ecotone-specific communities are generally distributed along physicochemical or microclimatic transition zones, such as gradients of salinity, moisture, or temperature. These gradients are referred to as ecoclines. As a result, ecotones are environments characterized by high biodiversity and are therefore particularly vulnerable to disturbances.

In most cases, plant and animal species from the two adjacent communities coexist within the ecotone; however, some organisms may be exclusive to the ecotone and absent from the neighboring ecosystems. In certain situations, the transition between two communities is abrupt and forms a well-defined boundary or edge, whereas in other cases it consists of a transitional one zone in which ecological conditions change gradually from one ecosystem to another.

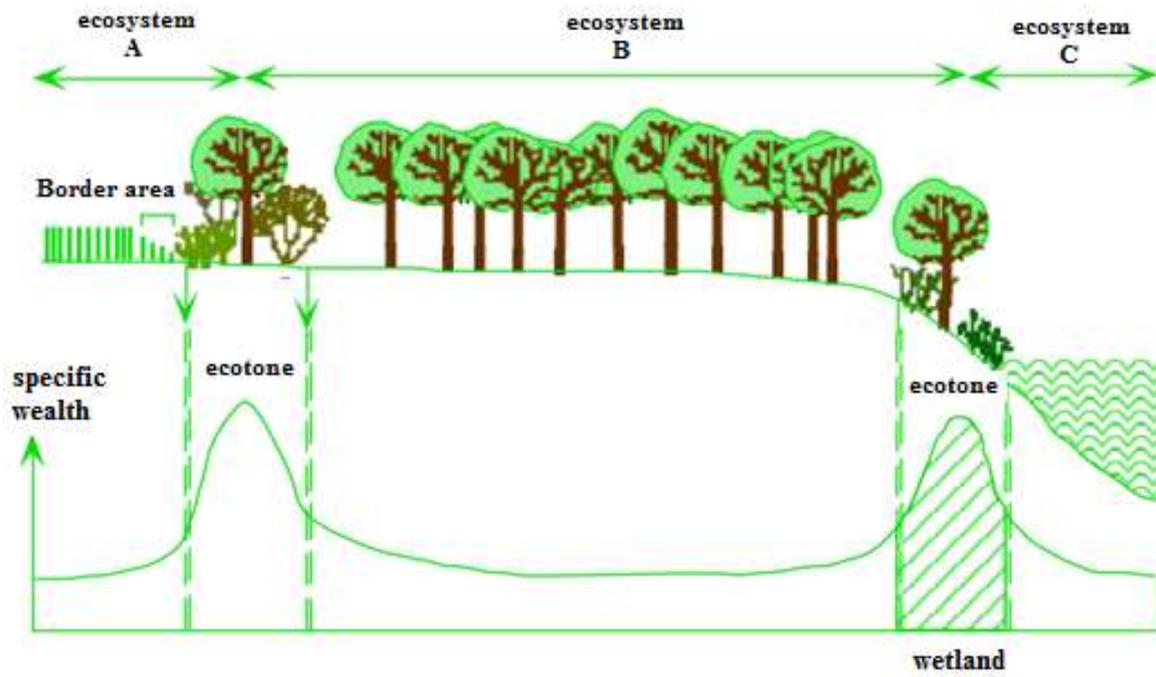


Figure 5.9. Diagram of the ecotone and its biodiversity (Amoros et al., 1993).

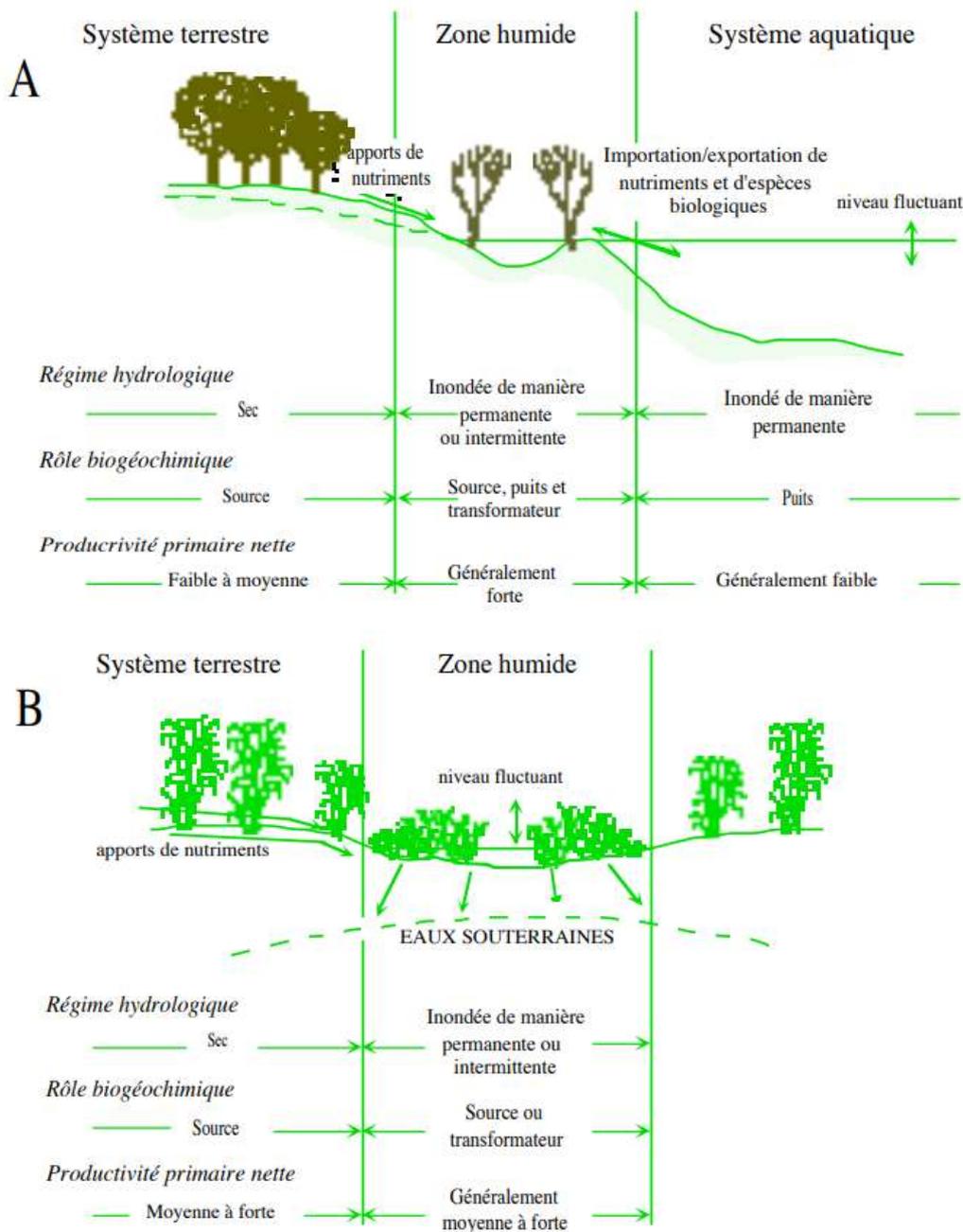


Figure 5.10. Wetlands may function either as part of a continuum between terrestrial systems and deep-water aquatic systems (A), or as systems isolated from any direct connection with open water bodies (B) (after Mitsch and Gosselink, 1993)

5.4 Concept of the ecocline

An ecocline is a gradient of physicochemical environmental conditions, determined by one or more key physicochemical factors that control living conditions and, consequently, the presence or absence of certain species. Ecoclines reflect continuous environmental variation rather than abrupt boundaries.

Examples of ecoclines include:

- **Thermocline:** a temperature gradient within a water body;
- **Chemocline:** a chemical gradient (e.g. oxygen or nutrient concentration) ;
- **Halocline:** a salinity gradient ;
- **Pycnocline:** a density gradient in water, induced by variations in temperature and salinity.

Ecoclines play a fundamental role in structuring biological communities, as species are distributed along these gradients according to their ecological tolerances and physiological requirements. They are therefore key elements in understanding species distribution patterns, ecosystem functioning, and the dynamics of transition zones such as ecotones.