Peatlands and marshes, remarkable wetlands

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Peatlands are wetlands whose vegetation produces peat that is very rich in organic carbon. The quantity of water entering the system and its chemical quality determine many types of peatlands or mires: acidic sphagnum bogs, alkaline fens, reed and large sedges marshes. Biodiversity is remarkable: many habitats, flora and fauna often in decline or with very particular adaptations, for example insectivorous plants or animals resisting to the cold. It is often necessary to ensure its conservative management. In addition, mires have other important functions: flood and low-water level regulation, carbon storage, various productions – reeds, peat, game, extensive livestock farming – and educational showcase. Peat also provides an environmental record of past vegetation, climate change and the chronology of certain human activities for the last 12,000 years after the glaciations.

1. Place of peatlands in wetlands

The definition of wetlands is complex, as it varies according to time, users or countries. The Ramsar Convention (1971) has a broad definition:"*wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres.*" [1]. It therefore includes coral reefs and Posidonia beds! These areas therefore form the interface between terrestrial ecosystems and the strictly aquatic ecosystems and are highly intertwined with them.

The definition of the *French Environmental Code* is more restrictive: *they are "lands, exploited or not, usually flooded or gorged with fresh, salty or brackish water permanently or temporarily; vegetation, when it exists, is dominated by hygrophilous plants for at least part of the year*" [2]. Both components are mentioned **(water** and **characteristic vegetation**), and a third - equally important - has been added to the application circulars: the **nature of the soil**, whose influence is fundamental.

Figure 1. "Sansouïres" of Camargue, a non-peaty wetland. [Photo © O. Manneville]

It is this nature of the soil that makes it possible to distinguish **peaty systems** (peatlands and most marshes) from other wetlands. By definition, a mire is a wetland colonized by vegetation growing on low-permeability soil and formed, at least in part, by peat to a thickness of at least 30 to 40 cm [3]. Salt flats (Guérande, Ile de Ré, France), salt marshes (Mont-Saint-Michel bay, Camargue, Figure 1) and various coastal or alluvial marshes, without peat, will therefore not be treated here, even if their interests in water or biodiversity are just as strong.

Wetlands, important ecosystems to be conserved. From this introduction, it should be stressed that all wetlands play many fundamental roles in the overall functioning of the planet; this theme will be discussed below. For various reasons, wetlands have been severely affected by human activities for about two centuries and this is why, over the past half century, many study or conservation programmes have been set up, from the regional to the international level [4].

2. Nature of peat and functioning of peatlands

2.1. Peat is a carbon-containing organic material

Peat consists of at least 20 to 30%, sometimes much more, of **poorly degraded organic matter**. The latter comes from the accumulation, over centuries or millennia, of plant residues (Bryophytes and higher plants) in an environment that is always full of water [3].

This permanence of water, which is stagnant or not very mobile and therefore highly depleted of oxygen, inhibits the activity of microflora and strongly slows down the decomposition and recycling of plant debris that led to peat formation. Peat, very rich in carbon-containing compounds, is at the same time a humus, a soil (called **histosol**) and an imperfect sedimentary rock rather close to coal. It can be extracted, either to constitute a poor performing fuel, or to fertilize various crops during its slow degradation in a drier and more oxygenated environment [3].

Figure 2. Illustration of two types of peat. On the left, blond peat with sphagnum moss in a core drill. On the right, black peat deriving from reeds and other plants, in a less acidic environment. [Photos © A. Laplace-Dolonde]

A peat or peat? There are many varieties of peat, depending on the accumulated plants and the physico-chemical conditions of accumulation (Figure 2). For example, blond peat comes from sphagnum mosses accumulated in an acidic (sometimes pH < 4) and rather cold medium. But not all peatlands are acidic or derived from sphagnum mosses, contrary to popular belief, and the pH can exceed 7 in plain or sea-side reed marshes.

Peat forms from bottom to top, the oldest levels being at the bottom of the peat bog. The **rate of accumulation** varies greatly from region to region and period to period, but is at an overall average of 1 mm per year, *i.e.* 1 m per millennium. With few exceptions, Europe's oldest current peatlands, which are about 11 to 12,000 years old, actually correspond to more than 10 m of peat.

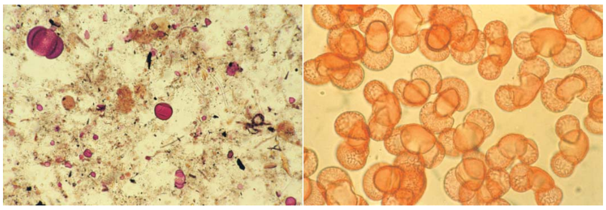

Figure 3. Plant debris extracted from peat (left) and pine pollen (right). [Photo © V. Vergne]

In addition, peat - and therefore peatlands - play an **environmental archiving** role at the end of the Quaternary period. Indeed, each level of peat retains for a very long time, especially thanks to anoxia, chemical compounds (e. g. lead), plant debris (pollen grains, sphagnum strands, tips of woody trunks; Figure 3) or animal remains (insects, gastropods) and protists. In addition, the carbon in the peat allows a fairly accurate dating by the C^{14} method. Thus, by combining, from the bottom to the top of a peat core, the chronology with the nature and abundance of these various markers, it is possible to reconstruct, since the end of the glaciations, the evolution of the regional climate, the dominant vegetation surrounding the prospected sites (borealtoundra{end-text}Discontinuous plant formation in cold climate regions, which includes some grasses, mosses and lichens, or even some dwarf trees (birches). The tundra is characterized by a ground perpetually frozen at depth (permafrost). It covers the far north of the Northern Hemisphere, before bare ground and ice, between 55° and 80° latitude.{end-tooltip}, taiga{ind-text}Forest-type plant formation traversed by a vast lake system resulting from fluvioglacial erosion. Strongly linked to the subarctic climate, it is one of the main terrestrial biomes. It is a transition zone between the boreal forest and the Arctic tundra.{end-tooltip} with pine and birch or beech wood) as well as the appearance of various human activities (clearing and cultivation in antiquity; use of lead in Roman times...) [3].

We have also found, very well preserved in peat for millennia, sacrificed human corpses, such as Tollünd's Man, in Denmark [10].

2.2. Distribution and origin of peatlands

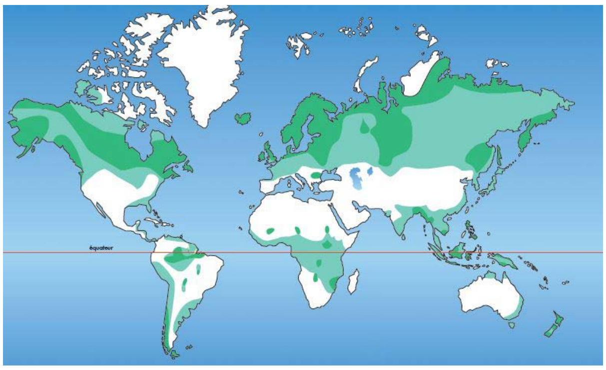

Figure 4. Global distribution of peatlands. Areas rich in peatlands are in dark green, medium to low in light green or very low in white. Source: Manneville, Vergne & Villepoux (2006), see ref. [3].

Observation of the global distribution of peatlands (Figure 4) shows two main types of biogeographical zones linked to particular climates and especially to water balance [3]. First of all, some **equatorial and humid tropical** areas (Amazonia, Indonesia and Malaysia...), where high temperatures prevail, but also heavy rainfall (several metres per year), have large areas of wooded peatlands.

The other type covers the **mid- to fairly high latitudes** of both hemispheres, in temperate or northern climates that are not too continental, with a higher density in Canada, the British Isles, Fennoscandia, the Baltic States and Russia, or -in the southern hemisphere- Patagonia, Chile and the Kerguelen Islands. At slightly lower and warmer latitudes, peatlands tend to take refuge in mountainous areas or oceanic areas; this is the case in France. These various regions have fairly moderate and highly variable temperatures over the seasons and receive between less than one metre to about two metres of annual precipitation. There are no mires in **extreme climates**, either desert that are too dry or very high latitudes and altitudes that are too cold.

The common point between these very varied peatlands is that **enough water** is needed to remain in the peat system; under a warm climate, a lot of rainfall is needed, while lower precipitation is sufficient under a cooler climate, because evapotranspiration{ind-text}A phenomenon characterizing the emission of water into the atmosphere, combining two phenomena: evaporation at ground level (which is a purely physical phenomenon) and plant transpiration (defined as water transfers in the plant and water vapour losses through leaf stomata).{end-tooltip} is lower there. Other favourable factors are the **topography** and **nature of the mineral subsoil**; incoming water must be stored for a long time, without flowing too quickly downstream or into a porous substrate. There are peatlands locally on ridges or slopes, or in filtering areas, but then cloudiness or spring inputs are almost constant.

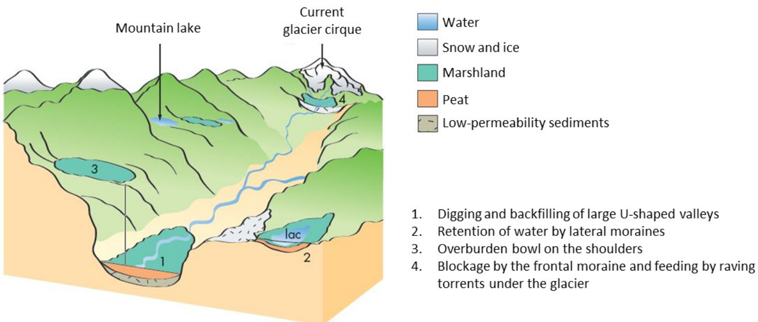

Figure 5. Influence of glaciers on the geomorphology and origin of peatlands. [Source: Manneville, Vergne & Villepoux (2006), see ref. [3]]

As mentioned above, most peatlands in France and Europe originated **after the retreat of the Quaternary glaciers,** mainly in the Holocene. During the glaciations, it was too cold and dry for the plants to develop properly. In addition, in frozen areas, glacier activity (erosion or morainal deposits) has scraped off older peatlands while creating a new relief favourable to the appearance of existing peatlands (in particular, the creation of many lakes or depressions and moraine deposits) (Figure 5). However, it should be noted that, contrary to what is sometimes said, many peatlands do not originate from a lake or pond!

Peat conditions the peatland system and the peatland produces peat! A remarkable feature of peatlands is that the plants that live there build the peat bog themselves by gradually accumulating their debris on which they live; once the process is initiated, some plants give rise to peat and the presence of peat allows the presence of these plants. They are therefore self-constructed ecosystems, which can undergo several successive evolutionary phases.

2.3. Peatland diversity and evolution

In reality, the diversity of mires and peatlands is very important, especially in France and neighbouring countries [3]. It is impossible to present all these types of peatlands here; only two very different and representative examples will be explained.

Figure 6. On the left, Lake Luitel with its floating mat and dwarfed pines - initial phase - and, on the right, the bog of the Luitel Pass, with sheathed cottongrass, Eriophorum vaginatum, and hooked pine, more advanced phase. [Source: © O. Manneville]

There are well-characterized peatland systems on the mountain level of our massifs. This is the case of the *Lac Luitel National*

Nature Reserve in France (Séchilienne, Isère, Belledonne crystalline massif, 1250 m) [5], which presents the archetype of **acidic sphagnum peatlands** from post-glacial lakes (Figure 6). All the stages of evolution, over millennia, are visible, from a lake bordered by a floating mat with sphagnum mosses and other specialized plants, to a reased mire or bog with sphagnum mosses and a wooded bog with hooked pine (Figures 6 & 7, [5]). Although there are water inflows from upstream of the bog, it is mainly rainwater, which is rather acidic and low in minerals, which conditions vegetation and peat production; this is called **ombrotrophic** feeding**.** Sphagnum mosses, which grow continuously upwards, produce peat by their dead parts, which raise the surface of the bog and permit the woody bog development. At this point, the groundwater completely escapes runoff and operates independently. Similar systems exist in the Vosges and the Pyrenees.

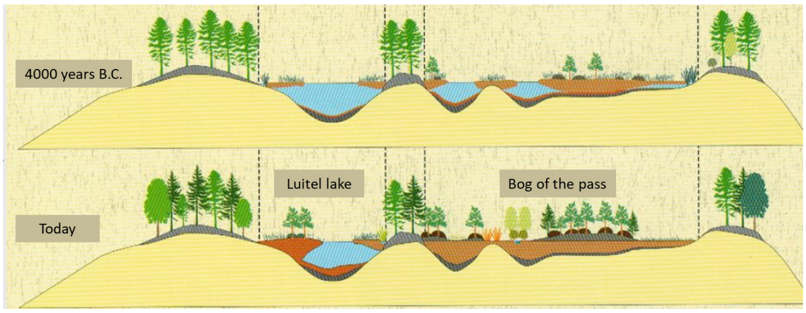

Figure 7. Two stages in the evolution of the Luitel bogs. [Source: Desplanque & Cave (2011), see ref. [5]]

Many bogs in the **Jura** follow a similar trend, but starting from fens originally fed by surface limestone waters [6]. The colder and wetter regional climate allows the peatland to gradually become more acidic, followed by an even greater raising than in the Alps. In all cases, these peatlands, subjected to constraining conditions (cold, poor substrate), have a flora and fauna close to the more northern European regions and have a relatively low productivity.

Figure 8. On the left, the Lavours marsh (Ain) at the foot of the Grand-Colombier. On the right, the marsh euphorb, Euphorbia palustris, a large plant of alluvial marshes. [Photos © O. Manneville]

The second example concerns large wetlands of plains or alluvial valleys. They are called **alkaline flat marshes**, but they also produce peat, of a different nature and origin from that of Luitel. We can mention the Brière (Loire Atlantique), the Vernier marsh (Eure), the Saint-Gond marsh (Marne) and the Lavours marsh (Ain) (Figure 8). The latter [7], originally several hundred hectares in size and located at an altitude of 230 m, is fed both by periodic flooding of the Rhône and its tributaries and by springs from nearby limestone massifs. It is a **minerotrophic** system, in which the direct role of rainfall is minimal; the underground water is calcareous, from pH 6 to 8, and enriched with minerals. There are silty mud levels interspersed in the peat, following the addition of river sediments. There are no sphagnum mosses, but many vascular plants (reeds, large sedges, alders and willows...) with high productivity, thanks to the hot microclimate and a higher trophic level (strong presence of NO_3^- ions). This has allowed the accumulation of more than 10 m of peat, black or brown, in 7000 years. But there is no raising, as the summer degradation of the litter above the groundwater is very rapid. Vegetation in the marsh no longer resembles that of the boreal regions, especially since many species in the ecosystems surrounding the marsh can colonize it (Figure 8).

In addition, France has various particular peat systems on the hills of the Armorican and Central Massifs, the Vosges or Corsica, without any initial body of water, or along the slopes in connection with seepage and springs or, again, in the back-littoral depressions of the sandy-silt coasts, from Dunkirk to Bayonne [3].

3. Peatlands and marshes are home to remarkable biodiversity

3.1. Each particular peaty habitat contains a special flora and fauna

Figure 9. On the left, a peaty habitat of community interest (alkaline dune depressions' fen with Schoenus) in Finistère (Brittany); on the right, a protected orchid, Liparis loeselii, in decline throughout Europe, living in this environment. [Photos © C. Manneville]

In addition to the diversity of peatlands between them, outlined above, there is the diversity of conditions within a single peatland, following various gradients, the most important of which depends on water. There is therefore a **biodiversity nested** at several scales; this explains the interest aroused by peatlands for scientists and naturalists, the complexity of understanding their functioning and the difficulties for the conservatory management of the many species that live or transit them (Figure 9). Moreover, peatlands evolve over time; it is therefore inevitable that their **habitats** (= microbiotopes and associated biocenoses{ind-text}All living beings that coexist in a given environment (the biotope). A biotope and its biocenosis are in constant interaction; they constitute an ecosystem{end-tooltip}) and their species appear or disappear cyclically.

The European Union protects its peatlands and their hosts. Many plant and animal species and habitats of wetlands, and of peatlands in particular, have become rare or threatened in Europe (Figure 9). The European Union's *Habitats-Fauna-Flora Directive* (1992) lists these threatened species and habitats; there is then an obligation for all States to implement protection or conservation measures. The *Muséum national d'histoire naturelle* has published Directive-related documents on the species and habitats present in France [8].

Rather than lists of species or illusory statistics, some groups of peatland and marsh species of biological interest are presented below.

3.2. Example of plant adaptations to nutrition problems

If, in peatlands, there is nothing to prevent a normal photosynthesis{ind-text}Bioenergetic process that allows plants, algae and certain bacteria to synthesize organic matter from the CO_2 in the atmosphere using sunlight. Solar energy is used to oxidize water and reduce carbon dioxide in order to synthesize organic substances (carbohydrates). The oxidation of water leads to the formation of O_2 oxygen found in the atmosphere. Photosynthesis is the basis of autotrophy, it is the result of the integrated functioning of the chloroplast within the cell and the organism.{end-tooltip} for plants, the permanence and characteristics of water slow mineral nutrition (cations and nitrate ions); here are three examples of adaptation to these constraints [3].

Figure 10. Butterwort leaves, Pinguicula sp., having trapped flies. [Photo © C. Manneville]

The lack of nitrates, caused by the anoxia of the substrate, has been solved by evolution, in a very original way by **carnivorous plants**, all of which living in peatlands or in standing water in Europe. Bladders, sunflowers and butterworts (Figure 10) have developed various types of traps that capture various arthropods, digest them with enzymes, and then directly absorb the amino acids that will be used to rebuild their own proteins.

Woody plants have developed another strategy for their nitrogen nutrition: symbiosis{ind-text}An intimate, lasting association between two organisms belonging to different species that results in beneficial effects for both. The organisms involved are referred to as symbionts or symbionts (anglicism); the largest can be named host.{end-tooltip} with other organisms. Thus, the Ericaceae (Figure 11) form underground mycorrhizae with various fungi capable of absorbing NH_3^+ ions which are toxic to most other plants, while the alder and the atlantic shrub *Myrica gale* host, in their root nodules, bacteria capable of directly fixing the molecular nitrogen dissolved in water (see Symbiosis & parasitism).

Figure 11. Sphagnum carpet housing an ericaceous flower, cranberry or Vaccinium oxycoccos, and rossoli, Drosera rotundifolia. [Photo © O. Manneville]

Sphagnum mosses (Figure 11) most often live in a very acidic environment (pH 5 or less) that is very low in cations. These mosses, storing water in special dead and empty cells, have the particularity of using proton pumps to exchange an mineral cation of the external water for an H^+ ion that exits. This allows them to feed; but the external pH decreases over time and this is unfavourable to other plants in the peat bog, which only compete poorly with sphagnum mosses! There are about 40 species of sphagnum moss in France and each one lives in a particular range of humidity and pH; it is well understood that they can replace one another gradually, as microconditions evolve. This contributes to the evolution of a floating mat into a raised mire, in addition to the accumulation of dead vegetation.

3.3. Some peatland animals [3]

Figure 12. Viviparous lizard, Zootoca vivipara, on a carpet of sphagnum moss. [Photo © Th. Delahaye]

Reptiles, cold-blooded animals, are disadvantaged, especially for their reproduction, in cold or wet ecosystems such as mires, especially in the mountains or in northern France. But the **peliad viper** and **viviparous lizard** have solved the problem: instead of laying eggs that will have trouble developing in the peatland, they give birth almost instantly to young ones who leave their shells to activate themselves. In addition, in peatlands, the peel of these animals is often very dark to be warmed by the sun and the blood of the viviparous lizard (Figure 12) may contain antifreeze substances that allow it to remain active during morning frosts, which are very common in almost all peatlands, even in summer.

Figure 13. On the left, Leucorrhiniadubia, a dragonfly of acidic mountain peatlands. On the right, a marsh butterfly, Maculinea nausithous, laying eggs on Sanguisorba officinalis. [Photos, left, © Christian Fischer (CC BY-SA 3.0), via Wikimedia Commons. Right, © ElliOrtner (CC BY-SA 4.0), via Wikimedia Commons]

Various **dragonflies** only live in cold bogs where their larvae must grow and feed in a harsh and poor environment. If necessary, these larvae wait three years in the water before metamorphosing into adults who will colonize new sites (Figure 13).

Some lowland alkaline marshes still contain butterflies of the genus *Maculinea* (azuré in French). The three species typical azurés of marshes, which have become rare in Europe and are therefore included in the *Habitats-Fauna-Flora Directive*, are present in the Lavours Marsh [7]. One's caterpillar feeds, at the beginning of its life, on *Gentiana pneumonanthe* flowers and those of the other two on the capitulas of the *Sanguisorbus officinalis* (Figure 13). In mid-summer, the caterpillars, a few mm long, fall to the ground where they can be recovered by ants of various *Myrmica* species. Thanks to chemical productions that are attractive to ants, caterpillars are introduced into anthills without being disturbed; they spend several months feeding on ants' eggs and larvae before metamorphosing in July to complete their cycle. This multi-partners system is very fragile, because if the host plant or host ant disappears, the butterfly will also disappear.

4. Importance and roles of these ecosystems: Need to conserve them

Figure 14. Winter flooding of the Cotentin and Bessin marshes (Manche). [Photo © A. Laplace-Dolonde]

For more than 50 years, the ecological (and therefore economic) importance of wetlands has been highlighted [3]. This concerns **water** first; basin head mires and alluvial plain marshes, by storing water in the peat, then slowly releasing it, slow down flooding and spread low water levels (Figure 14). In addition, the water is filtered and purified through its passage through the peatlands and the plants that cover them.

Interest in **biodiversity** is fundamental (see above), as well as in various productions (reed harvesting, hunting, freshwater fishing, extensive livestock farming). Let us also recall the production of **peat** as well as **environmental archiving** and add historical, traditional cultural, recreational and educational aspects [3],[7].

Figure 15. Fire in a peat bog in Mont-Saint-Michel area. [Photo © A. Laplace-Dolonde]

The Earth's peatlands store carbon and slow down the greenhouse effect. All the peat accumulated on Earth over thousands of years contains about 500 gigatonnes of carbon (5 x 10^{11} tonnes), the equivalent of seventy years of anthropogenic greenhouse gas emissions [9]! Peatlands cover 3% of the Earth's surface, but store twice as much carbon as all forests combined. However, drainage or global warming causes peat to decompose and melt, followed by the release of CO_2 and CH_4 into the atmosphere. The dramatic effects of peatland fires (Figure 15) are also noteworthy, both in Siberia and in Malaysia and Indonesia. (see A Carbon cycle disrupted by human activities).

It is estimated that, over the past 200 years or so, between **50 and 75% of** peatlands (and other wetlands) have been **destroyed or severely degraded** in France and neighbouring countries. For peatlands, there are many causes:

- drainage for corn cultivation or poplar and conifers planting;
- industrial peat extraction that totally destroys the ecosystem;
- flooding to create ponds or hydroelectric dams;
- backfilling through landfills, the extension of urban areas or transport and energy infrastructures;
- various types of pollution, including latent eutrophication that accelerates the decomposition of peat.

A late awareness, sometimes thwarted by a strong inertia in decision-making, has emerged to conserve what remains and restore as many peatlands and marshes as possible [4]. In France, with respect to biodiversity and natural habitats, the so-called *Pôle-relais national Tourbières* in Besançon is responsible for collecting and disseminating knowledge and know-how to the various french managers such as natural parks, nature reserves, conservatories and various local authorities.

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Cover image. Lake Luitel (Isère, France) in autumn, with its floating mat with red sphagnum mosses. [Source: Photo © A. Lemercier]

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