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Assessment of the dynamic trajectories and maritime character of Armorican cliff-top coastal heathlands

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Abstract

Atlantic coastal cliff heathlands are chamaephytic vegetation dominated by *Ericaceae*, most often associated to *Fabaceae* (*Ulex*) and integrated from a phytosociological point of view into alliance of *Dactylido oceanicae-Ulicion maritimi* Géhu 1975 (class of *Calluno vulgaris-Ulicetea minoris* Braun-Blanq. & Tüxen ex Klika & Hadač 1944). This alliance gathers coastal heathlands under marine influences whose physiognomy is marked by prostrate or halo-anemomorphic chamaephytes. All Atlantic heathlands are included into habitats of European community interest which justify the designation of Natura 2000 sites. Within these protected areas, heathland conservation or restoration management issues raise the question of the choice of nature and frequency of management methods. For that, it seems important to understand the dynamics of cliff-top coastal heathlands. Stable heathlands, considered as permanent vegetation of primary character, can be managed without any intervention, while heathlands characterized by a progressive dynamic may be subject to interventionist management. The aim of this work is to present the main determinant abiotic and biotic factors driving the cliff-top coastal heathlands. Human uses may influence the composition and structure of these vegetation. This approach helps to assess the primary or secondary character of cliff-top coastal heathlands vegetation, their stability or dynamic. This article clarifies the notions of primitive, primary and secondary coastal heathlands. It proposes criteria to differentiate stable heathlands and unstable heathlands which are characterized by a progressive dynamic towards coastal scrublands or forest: abiotic conditions, floristic combination, physiognomy. The synphytosociological methodology is useful for establishing the typology of the series, permaseries and minoriseries, in which the different types of cliff-top coastal heathlands are included.

Keywords

Armorican Massif, cliff-top coastal heathlands, human influence, synphytosociology, vegetation dynamics

Introduction

Heathlands are generally assimilated to formations structured by chamaephytes and dwarf nanophanaerophytes (Gimingham et al. 1979). They constitute low ligneous vegetation such as scrublands, "maquis" and certain *Cytisus* Mediterranean vegetation (Rivas-Martínez 1979; Díaz González 1998; Géhu 2006).

Floristically, heathlands are dominated by evergreen and scleromorphic species (Specht 1979; Ellenberg 2009), both on dry and humid soils, in hot or cold climates (Warming 1909). They are characterized worldwide by the presence of taxa of the Ericales order and in Europe by the more specific presence of *Ericaceae* (Gorissen 2004; Loidi et al. 2010). In the Atlantic region, heathlands are characterized by the joint presence of *Fabaceae* (mainly *Ulex* species) and *Ericaceae* (*Erica* species and *Calluna*).

Two main sets of heathlands can be distinguished:

- (sub) primary or (sub) climacic heathlands in equilibrium, with strong natural constraints such as wind, salt spray deposition, prolonged periods of frost, avalanches or erosion (Morand 1971; Géhu and Géhu-Franck 1975), or instability of the substrate. They can be located on coastal cliffs and headlands and subalpine and alpine areas;
- secondary heathlands, most often regressive, which are, conversely, strongly influenced by human uses. They have replaced the primary climacic "savannah" or forest. They are generated by two main types of

disturbances. On the one hand, agropastoral actions, which, after an initial period of deforestation, favored the maintenance of a heathland by mowing, grazing or fire (Webb 1998; Loidi et al. 2010); on the other hand (agro-)sylvicultural disturbances which allowed the establishment of heathlands within acidiphilic forest systems. These heathlands are dynamically situated between grasslands (or oligotrophic meadows) or preforest edge vegetation which can evolve towards scrublands or forests. Some secondary heathlands can also be metastable, following extreme soil impoverishment, preventing or at least slowing down the establishment of trees on a human scale (plagioclimax, paraclimax or disclimax).

Armorican cliff-top coastal heathlands are part of Atlantic heathlands on the western most side of Europe. They are found in the British Isles, France, northern and western Spain and Portugal, up to Atlantic northern Moroccan coast (Gimingham 1972; Deil et al. 2010; Loidi et al. 2010). Their presence further north, on the North Sea coast, as part of a gradual transition to the boreo-alpine heathlands, remains to be studied. Armorican cliff-top coastal heathlands are characterized by the presence of halo-anemomorphic ecotypes, in particular prostrate gorses represented by *Ulex europaeus* L. subsp. *europaeus* f. *maritimus* (Hy) Cubas and *Ulex gallii* Planchon subsp. *gallii f. humilis* (Planch.) Cubas and maritime broom *Cytisus scoparius (*L.) Link subsp. *maritimus* (Rouy) Heywood.

Armorican cliff-top coastal heathlands are integrated within the alliance *Dactylido oceanicae-Ulicion maritimi* Géhu 1975, order *Ulicetelia minoris* Quantin 1965, class *Calluno vulgaris-Ulicetea minoris* Braun-Blanq. & Tüxen ex Klika & Hadač 1944 . On the synphytosociological level, two points of view do exist. First, cliff-top coastal heathlands can appear directly on bare ground, without being preceded by a grassland stage. Under these conditions, heathlands constitute both pioneer and terminal stages of vegetation series. They constitute single-stage vegetation series, as a "halo-anemogenous coastal rock permaseries" (Loidi et al. 2011; Loidi 2021). The second point of view considers that the absence of associated grasslands does not mean that they did not previously exist and the reduction of climatic constraints like in the more sheltered sectors, allows the appearance of scrubs species or bracken communities. In addition, the ancient agropastoral on coastal cliffs has to be considered. This is why some authors, such as Demartini et al. (2017), consider coastal heathlands of *Dactylido oceanicae-Ulicion maritimi* as vegetation included in minoriseries.

The Armorican Massif is a geological entity located in the western most part of France and Europe, encompassing the Channel islands, Brittany, western Normandy, a large part of Pays de la Loire. The studied cliffs are located in departments of Loire-Atlantique, Ille-et-Vilaine, Morbihan, Finistère, Côtes-d'Armor and Manche. On the coastal cliffs of the Armorican massif, depending on the intensity of abiotic influences and the historical presence of sedentary humans, some heathlands seem stable, especially on large rocky promontories. In sheltered conditions, moderately exposed to sea winds, they can evolved towards dense scrubs or coastal forests.

Stress and disturbance maintain the structural and species diversity of heathland vegetation. As highlighted by Clément (1987), stress corresponds to the influence of an external factor, abiotic or biotic, which reduces the rate of dry matter production of vegetation. The determining abiotic factors structuring cliff-top coastal heathlands are:

- *climatic conditions*: salt spray deposition combined with frequent and often strong winds (Malloch 1972; Parson 1981; Griffiths and Orians 2003a), which causes water stress and burns plants, and whose effect is accentuated by the low water availability (Griffiths and Orians 2003b). These climatic conditions determine the morphological and physiognomic originality of the Armorican coastal heathlands (Géhu 1975) linked to the presence of numerous ecotypes and coastal accommodate species (Corillion 1965). Fullerton (1998) proposes the term "cliff-top coastal heathlands";
- *nature of the substrate*: an essential factor is the physico-chemical characteristics of soils (Clément 2008a). The heathlands are favored by oligotrophic and often acidic soils, generally lithosoils, rankosoils or podzosoils. All geological substrates little altered or releasing little fertile material after alteration, are favorable to heathlands. Phosphorus deficiencies and aluminum toxicity are part of the soil constraints (Clément 1987).

Along Armorican coasts, remains of anthropogenic uses are omnipresent on the coastal heathlands (low walls, paths, mounds, ditches, barred spurs, prehistoric and protohistoric remains, seaweed ovens, etc.). They testify that these environments have been grazed, harvested and sometimes sown. They were integrated into peasant life until the end of the XIX[th] century and have persisted in certain sectors, thanks to a multi-livestock activity that lasted until the middle of the XX[th] century. Gorse has held a relatively important place in the economy of the peasantry and in its oral traditions.

Environmental factors driving cliff-top coastal heathlands are the resultant of abiotic stress and anthropogenic disturbance (Fig. 1). Concerning past activities, some issues remain to be discussed. What is the real influence of these human disturbances on vegetation? If the disturbance is low and the vegetation not very dynamic, are there long-term consequences? Did agropastoral activities condition the evolution of cliff-top coastal heathlands, and did their abandonment result in the appearance of progressive dynamic indicators?

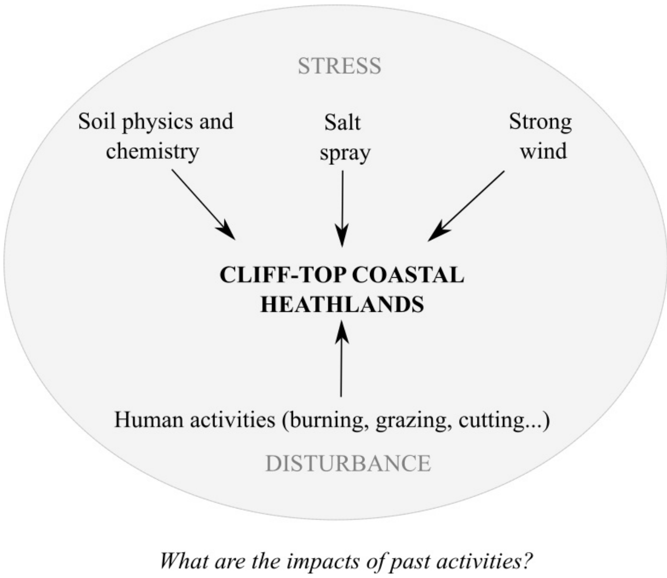

Figure 1. Environmental factors of cliff-top coastal heathlands.

Theoretical concepts on vegetation successions of coastal heathlands

We propose to discuss vegetation dynamics concepts regarding coastal heathlands.

This approach concerns cliff-top coastal heathlands on rocky substrates in the Armorican massif. It does not analyze dune heathlands on sandy soils which may be the subject of future similar work.

Primitive cliff-top coastal heathlands

Primitive cliff-top coastal heathlands represent a vegetation existing before any significant human intervention, therefore before the Neolithic (Géhu 2006). The heathlands most exposed to wind and salt spray deposition on lithosoils may be primitive vegetation. Concerning the possible preex-istence of coastal forested heathlands, charcoal research studies are in progress in Armoricain Massif (Brittany, France) (Glemarec and Bioret 2021). These historical elements will contribute to the hypothesis of a secular succession and long-term changes, often climate change.

Primary cliff-top coastal heathlands

This type corresponds to heathlands whose existence and appearance are not linked to human actions effects. It corresponds to maritime heathlands whose dynamics are naturally blocked. If extensive grazing or irregular mowing are present, they may have little influence on the natural dynamics of theses heathlands. They appeared following the colonization of bare soil, after a possible grassland stage, but did not result from deforestation.

A primary heathland appears from primary succession. They are characterized by a spatio-temporal "heathland continuity" differentiated by total absence of human intervention (e.g. grazing, mowing).

Primary succession occurs on recently bare substrates (Hull et al. 2018), with generally low nitrogen and which implies that nitrogen-fixing organisms are important in the early stages (Gorham et al. 1979). This is not the case with rankosoils on acidic substrates where aluminum ions are free and bind phosphate ions, making them less available to plants. Thus, in heathland soils, the average amount of phosphorus is thirty times lower than in brown forest soils (Clément 1987). Heather has a good ability to capture this chemical element, in particular thanks to its extensive roots net-work and its mycorrhizal symbiosis (Pearson and Read 1973; Malajczuk and Lamont 1981). Gorse, on the other hand, is able to fix atmospheric nitrogen thanks to the nodules present on its roots. These nodules are the site of symbiotic activity and the production of amino acids (Reid 1973). The heathlands are therefore capable of directly colonizing very poor soils and can thus settle over time, especially when edaphic and climatic conditions are too constraining. This is the case of the Armorican coastal cliffs whose geological substrates (i.e. granite, sandstone) release few fertile elements and conditions of exposure to wind and salt spray deposition favor heathlands.

Secondary coastal heathlands

Secondary coastal heathland is the result of human interventions (trees or shrubs cutting, intensive grazing, burning, removal of soil, quarries). Heathlands represent the preferential successionnal stage after deforestation of meso-xerophilic or meso-hygrophilic coastal forests. Inland heathlands are induced by the same process. Secondary successions refer to the changes in specific composition that return a disturbed community to some semblance of its original composition (Horn 1974). This is the "recovery of a mature community from major disturbance by natural agents […] or after human impact such as burning and clearing […] or a vegetation development following a specific sequence of events […] followed by a different type of use" (Glenn-Lewin and van der Maarel 1992). These successions occur on substrate that is totally or partially intact, and consequently they occur more rapidly (Hull et al. 2018). Gorses and heathers of coastal heathlands colonize the open spaces following deforestation, as these species do in the inland heathlands. Colonizing species are located in neighboring communities or are confined to unforested rocky outcrops. Previous vegetation elements may persist as seed bank or seedlings (Sawtschuk 2010) and may explain the presence of forest species in secondary coastal heathlands.

Progressive and regressive dynamics, natural or artificial

According to Molinier and Vignes (1971), the evolution of natural environments is progressive or regressive, natural or artificial. The gradual evolution consists in the increase in the number of layers in vertical structure of vegetation and in composition of the soil. It is generally spontaneous and slow (auto dynamics). Human uses sometimes accelerate the forestation process. The regressive trend results in a decrease in the number of layers, most often caused by cutting, fire and overgrazing.

Degradation of coastal heathlands can lead to the development of secondary grasslands which differs probably from the primary community, if there was one. Excessive burning or grazing of inland heathlands (Clément and Touffet 1981; Rosa García et al. 2012) and the use of artificial fertilizers (Aerts and Heil 1993) change vegetation into grassland. This process should be probably similar for coastal heathland.

The progressive dynamic stage on coastal heathlands is the development of coastal scrubs with maritime gorse (*Ulex europaeus* subsp. *europaeus* f. *maritimus*), blackthorn (*Prunus spinosa* L.) and Plymouth pear (*Pyrus cordata* Desv.). In disturbed coastal heathlands linked to agriculture, trampling, soil enrichment, etc., scrublands have a different composition: high abundance of brambles (*Rubus* sp.), scarcity of maritime gorses, allogenous thickets.

Climacic coastal heathlands

The first definition of climax, proposed by Clements (1936), is a state of equilibrium towards which an ecosystem tends. The climate determines the development of plant communities; soil and topography influence their composition. This is "a stable association of species which qualitatively and quantitatively characterizes the final stage of development of a biocenosis in succession" (Ramade 1984). Climacic heathland can be considered in balance by climate, soil, topography; it represents the terminal stage of progressive evolution of vegetation.

On a human scale, even over several generations, some coastal cliffs heathlands seem stable. Authors (Lemée 1938; Corillion 1971; Morand 1971; Géhu 1975; Gloaguen 1988; Hardegen and Bioret 2000) suggest that in hyperoceanic temperate areas of the coast of Armorican Massif, coastal heathlands may become the climax, the vegetation being too constrained by soil, wind and salt spray deposition.

The hypothesis is that coastal cliffs could have been grazed or mowed, but these agricultural practices did not disturb the soil neither the natural dynamics of the heathlands. Natural impoverishment of the soil (erosion, podzolization) and/or the strong wind and salt spray deposition are causing stability of cliff-top coastal heathlands. This is different from the notion of paraclimax (plagioclimax or disclimax) (Couderc 1971). This concept of paraclimax is perfectly adapted to heathlands, particularly inland ones, on acidic and oligotrophic soils. This oligotrophy, due to a long past of mowing, burning, grazing, etc. is causing very low progressive dynamics and almost metastability, especially on the most acidic rocks (Clément 2008b). Heathland can constitute "a plagioclimax community dependent on man-induced activities to maintain dwarf shrub vegetation and to prevent secondary succession to woodland" (Webb and Vermaat 1990).

The difficulty of considering the climacic state is the spatio-temporal scale of a reference. A disturbance, such as the loss of single individual plant, may cause a micro-successional sequence if that individual is predictably replaced by another species with other ecological attributes (Hull et al. 2018). On a precise scale, these micro-disturbances can appear as signs of dynamics towards other vegetation. On a larger scale, these micro-disturbances can be considered as a component of equilibrium of the climatic vegetation, as a cyclic succession in the sense of Gimingham (1972).

In coastal conditions, punctual abiotic stress or human disturbance can lead to localized settlement of isolated scrubs or linear grasslands that can not be considered as long term dynamic indicators.

Proposed definitions of Armorican coastal heathlands types

By taking into consideration physiognomical, ecological and dynamical features, we propose to distinguish four types of Armorican cliff-top coastal heathlands:

- three maritime heathlands under strong maritime conditions: (1) Maritime grass-heathlands; (2) Cushion shaped maritime heathlands; (3) Medium sized maritime heathlands. The semantic "maritime"

is used because the principal ecological factor is the proximity of the sea;
- one type of coastal heathlands under moderate maritime conditions: (4) Retro-coastal heathlands. The semantic "retro-coastal" is used because their dynamics are mainly driven by edaphic conditions.

Table 2 presents differential criteria of types of coastal heathlands.

(Cliff-top) Maritime grass-heathlands

Maritime grass-heathland (Fig. 2) is structured as a homogeneous vegetation, mono-stratified (a single vegetation layer < 30cm), developed under edaphic constraints (superficial lithosoils or meso-xeric rankosoils of variable thickness, with outcropping rocks) and exposed of marine climatic factors (wind, salt, erosion, drought; distance to the sea less than 100 m). The floristic composition combines the presence of halo-anemomorphic grassland transgressive plant species (*Festuca huonii* Auquier, *Festuca rubra* subsp. *pruinosa* (Hack.) Piper, *Daucus carota* subsp. *gummifer (Syme)* Hook.f., etc.) and *Ericaceae* (*Erica cinerea* L., *Calluna vulgaris* (L.) Hull). This heathland type develops topographically at the upper contact of halo-anemomorphic grassland and at the lower contact of maritime gorse vegetation. Areas covered by this type of heathland are mainly over several hundreds of square meters. It can be considered as an ecotone expressing a spatial transition plant community, or as a real community entity, stable and mappable. Various studies, in particular Fullerton (1998), conclude that this non-shrub based structure has utility for classification of cliff-top coastal heathlands. In this sense, Coombe and Frost (1956) designated *Festuca ovina-Calluna* heath ('Rock Heath') on Cape Lizard. This compartment of Maritime grass-heathlands is described in Brittany, at the pointe of Dinan in Crozon as "heathland (which) begins with a very grassy formation (lande (qui) débute par une formation très herbeuse)" (Géhu 1963a) and on Cap Fréhel as "grass-heathland (pelouse-lande)" (Forgeard et al. 1980). On this latter site, Géhu (1963a) writes, concerning this compartment of vegetation: "This (vegetation) is undoubtedly not only

Figure 2. Maritime grass-heathlands *Festuca huonii-Erica cinerea* community. Cap de la Chèvre – Crozon (top) / Kastel Koz – Beuzec Cap Sizun (bottom).

a mixture and a mosaic of species of *Armerion maritimae*, *Ulicion gallii* and *Sedion anglici*, it is also, it seems, a marginal rocky community of natural heathland (Cet ensemble n'est sans doute pas seulement un mélange et une mosaïque d'espèces de l'*Armerion maritimae*, *Ulicion gallii* et *Sedion anglici*, c'est aussi, semble-t-il un groupement rupestre marginal, de la lande naturelle)".

(Cliff-top) Cushion shaped maritime heathlands

Shaped by wind and salt spray deposition (distance to the sea less than 250 m), Cushion shaped maritime heathlands (Fig. 3) are low-growing (one vegetation layer < 50 cm). Chamaephytes present necrosis band facing the sea. This vegetation is mono-stratified, gorses (*Ulex europaeus* subsp. *europaeus* f. *maritimus* and *Ulex gallii* subsp. *gallii* f. *humilis*) and heathers reaching more or less the same size. The most halo-anemomorphic form present bare soil gaps colonized by transgressive grassland species.

This type of heathland presents stability at the scale of vegetation community and landscape. However, there is an intern dynamic in the community. In the example of the *Scillo vernae-Ericetum cinereae* Bioret 1994 heathland, *Calluna vulgaris*, which presents necrosis due to salt spray deposition, protects *Erica cinerea*. Depending on variations of the winds and salt spray deposition intensity, chamaephytes present cyclic successions over time, with stable representation of individuals over the long term. Fig. 4 shows monitoring carried out on this type of heathland for ten years.

(Cliff-top) Medium sized maritime heathlands

Also conditioned by strong maritime conditions (distance to the sea less than 500 m), Medium sized maritime heathlands (Fig. 5) are structured by a layer between 0.6 to 1 m high. Chamaephytes are shaped by the wind but don't present necrosis due to salt spray deposition. This vege-

Figure 3. Cushion shaped maritime heathlands *Scillo vernae-Ericetum cinereae* Bioret 1994. Porz Doun – Ouessant (top), Cap de la Chèvre – Crozon (bottom).

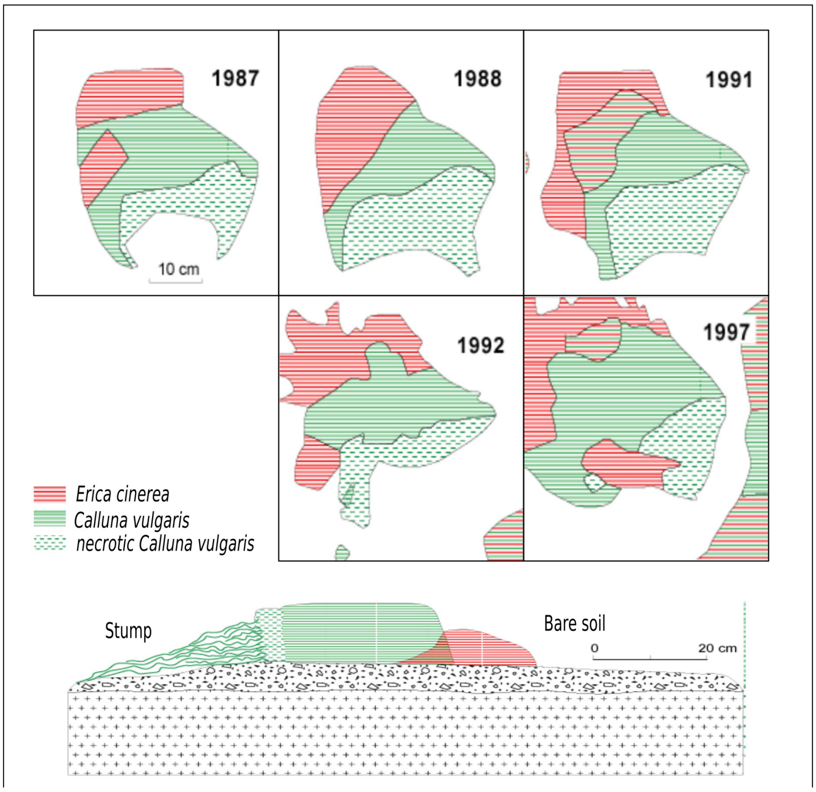

Figure 4. Cyclic succession and dynamic stability of *Calluna vulgaris* and *Erica cinerea* in S*cillo vernae-Ericetum cinereae* on the island of Ouessant (1987-1997) (F. Bioret, unpublished data).

tation is mono-stratified, gorses (*Ulex europaeus* subsp. *europaeus* f. *maritimus* and *Ulex gallii* subsp. *gallii* f. *humilis*) and heathers (*Erica cinerea*, *Calluna vulgaris*) reaching more or less the same size in strong maritime conditions. Vegetation is paucispecific and halo-anemomorphic grasslands transgressive species are generally absent.

In retreat from the top of the cliff, where direct wind and salt spray deposition influence decrease, Medium sized maritime heathland can evolve towards scrubland. *Ulex europaeus* subsp. *europaeus* f. *maritimus* and *Prunus spinosa* scrub can constitute a serial mature stage.

Retrogressive grasslands may be present, dominated by *Festuca* gr. *ovina* (*Festuca huonii*, *Festuca filiformis* Pourr., *Festuca guestfalica* subsp. *ophioliticola* (Kerguélen) Boeuf et al. on serpentine bedrocks) or *Dactylis glomerata* L.. They are linked to erosion, occasional eutrophication, soil modification, rabbit warrens or seabird colonies.

This type of maritime heathland is facing similar oceanic exposure conditions and its physiognomy is comparable to the maritime scrublands with *Ulex europaeus* subsp. *europaeus* f. *maritimus* or *Ulex gallii* subsp. *gallii* f. *humilis* (*Sileno maritimae-Ulicetum maritimi* Géhu 2007, *Silene maritima-Ulex gallii* f. *humilis* community, *Helianthemo nummularii-Ulicetum maritimi* Bioret, N.Caillon & Glemarec 2014, *Peucedano officinalis-Ulicetum maritimi* Bioret, N.Caillon & Glemarec 2014, *Schoeno nigricantis-Ulicetum maritimi* Bioret & Davoust 2000, *Rubio peregrinae-Ulicetum maritimi* Bioret 2008). Presence or absence of heathers is determined by edaphic conditions.

Retro-coastal heathlands

On the coast, in semi-exposed mode, next the sea, sheltered from too strong wind and salt spray exposure (distance to the sea less than 500 m in exposed cliffs to high maritime conditons) Retro-coastal heathlands (Fig. 6) differ from other types of maritime heathlands by the presence of higher chamaephytes accompanied by pre-forest species which indicate a potential succession towards forest. Over wind influences, thin soils represent the main driver of the dynamic of these heathlands, which are mainly present on rocky outcrops. *Erica cinerea* is always present, while *Calluna vulgaris* is rare. Maritime form of *Ulex europaeus* subsp. *europaeus* is only represented by "ball" type (Godeau 1985) which cannot be systematically related to the maritimus form.

Landicolous chamaephytes are accompanied by forest edges species, mainly *Teucrium scorodonia* L., *Hedera helix* L. (or *H. hibernica* (G.Kirchn.) Bean), *Rubus* sp. (cf. *ulmifolius* Schott), *Lonicera periclymenum* L., *Agrostis capillaris* L. (or *Agrostis* x *murbeckii* Fouill.), *Polypodium interjectum* Shivas. This type of heathland is sheltered from hyper-oceanic conditions, characterized by absence of halo-anemomorphic taxa and dynamic potentiality directly influenced by edaphic conditions.

Structurally, Retro-coastal heathlands are characterized by two layers with high gorses, or one layer > 1m. This heathland is most often present in mosaic with scrublands or coastal forests. It finds its optimum on cliffs sides and rocky promontories slightly exposed to maritime conditions and in the bays, abers or rias. Today, these heathlands can be only found on thin soils and their dynamics remain slow.

Retro-coastal heathlands have affinities and compositions close to the hyper-Atlantic heathlands of the rocky spurs of the inland. They can be differentiated from them by the anemomorphic "ball" form of *Ulex europaeus* subsp. *europaeus*.

Additional elements of understanding dynamics of Armorican cliff-top coastal heathlands

Autogenic, allogenic and anthogenic succession in cliff-top coastal heathlands

Autogenic succession is a change in vegetation resulting from biotic interactions and biotic changes in the environment (Tansley 1935). It mobilizes "internal" mechanisms as competition or modification of the soil by plants. In the long term, pioneer maritime grasslands can allow gorse development by stabilizing the soil.

Allogenic succession is a change in vegetation due to environmental conditions or "external" forces that alter balances. The evolution of vegetation due to climate change is an example (Glenn-Lewin and van der Maarel 1992). Under changes in micro-climatic conditions, or the reduction in the frequency of climatic events such as salt spray deposition and strong wind, maritime heathlands can evolve towards maritime scrublands.

Secondary dynamics of vegetation can be qualified of allogenic succession due to abiotic factors and anthogenic succession induced by human actions. Anthogenic succession concerns part of Medium sized maritime heathlands resulting from pastoralism and Retro-coastal heathlands resulting from the removal of scrubs and tree cutting.

Dynamic of Maritime grass-heathlands and Cushion shaped maritime heathlands

Maritime grass-heathlands and Cushion shaped maritime heathlands are the most constrained vegetation by exposure to marine conditions and nutrient-poor soils (high

Figure 5. Medium sized maritime heathland *Ulici humilis-Ericetum cinereae* (Vanden Berghen 1958) Géhu & Géhu-Franck 1975. Cap Fréhel – Plévenon (top), Bremeur - Goulien (bottom)

acidity, very little phosphorus availability). Today they seem stable and do not show dynamics without human interventions.

Dynamic of Medium sized maritime heathlands

This maritime heathland can either be the mature stage of dynamic of the vegetation or constitutes a serial stage towards a maritime scrubland with scrubs such as *Prunus spinosa*. It depends on the use or composition of the soils or on the intensity of maritime conditions. *Dactylis glomerata* (incl. subsp. *oceanica* G.Guignard) or *Festuca* gr. *ovina* grasslands are secondary and linked to an opening of the vegetation by human or animal actual or ancient actions.

There is no natural dynamic link to Maritime grass-heathlands or Cushion shaped heathlands (except climate change and reduction of maritime conditions).

The question on their probable very long-term evolution towards a forest or their apparition after old clearings remains open. Maritime abiotic conditions, associated with thin soils and summer drought, lead to a high stability of maritime heathlands or scrublands.

Edaphic factors are essential. Thickness of the soil and its degree of acidity influences the biomass production: edaphic conditions are more restrictive for thin soils on sandstone than for deep soils on micaschists (Fig. 7).

Dynamic of Retro-coastal heathlands

Retro-coastal heathlands are probably the result of old deforestation of coastal forests located on the headland or on the slopes of the coastal cliffs and favored by moderate maritime conditions. When the forest disappears consecutively to human activities, the Retro-coastal heathland surface is correlated to the area of cutting, burning, etc. The Retro-coastal heathlands then naturally evolve towards Retro-coastal scrublands. This development may be constrained by pastoral activity that maintains the heathlands. If pastoral activity is intensive, Retro-coastal heathlands can evolve towards open grasslands. Without excessive erosion linked to human or natural uses (wind, drought, rain, storm), grassland can re-evolve towards heathland. The rapidity of recolonization of woody vegetation depends on the degree of exposure to maritime conditions on the trophy of the soil. Retro-coastal heathlands

Figure 6. Retro-coastal heathlands *Teucrium scorodonia-Erica cinerea* community. Pointe de Primel – Plougasnou (top), Pointe de Plouha - Plouha (bottom).

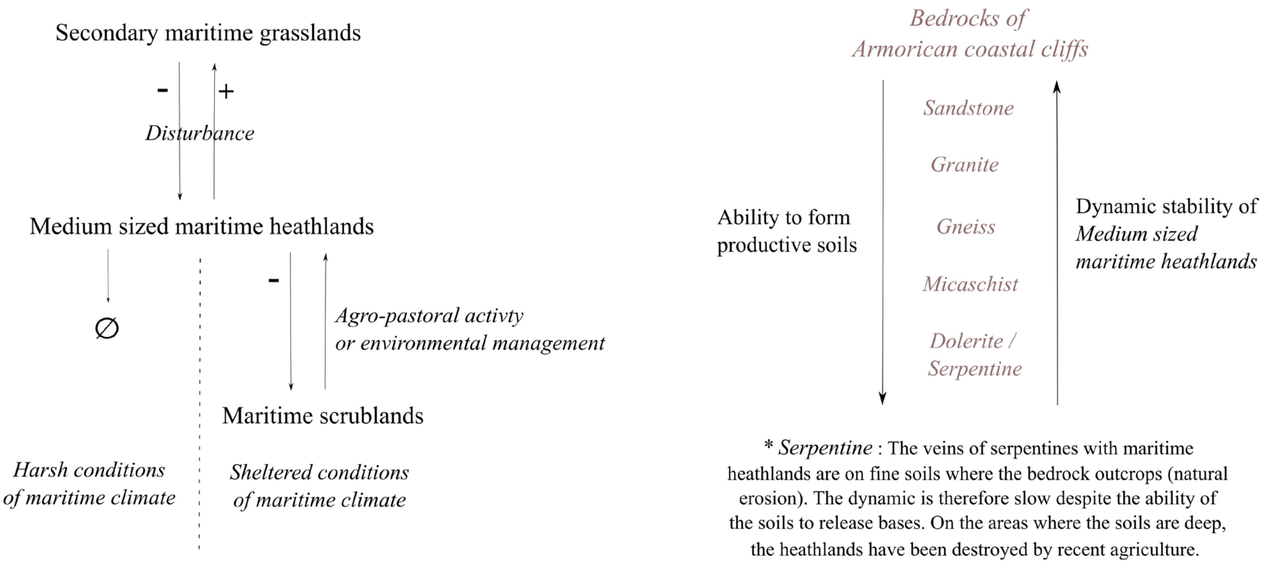

Figure 7. Dynamics of Armorican Medium sized maritime heathlands: influence of climate, agropastoral activities, bedrock and soil

can re-evolve into a Retro-coastal scrublands and coastal forest. Edge forest plants present on the different dynamic stages can be considered as relicts of the coastal forest.

The Retro-coastal heathlands can be structured by micro-patches of dynamic vegetation. They constitute small homogeneous areas. In a small patch of vegetation, micro-environmental conditions are similar and may vary from the surrounding environmental conditions. The main drivers linked to the constitution of such patches are the history and the current regime of disturbance (Forman and Godron 1981): grazing, firewood cutting and climatic hazards (storm, drought, etc.).

Vegetation influences micro-environmental conditions, soil constitution, local protection from exposure to wind and salt spray deposition. The development of low scrubs favors the establishment of tall scrubs. A dynamic towards the forest is ongoing. This slow evolution is inversely proportional to the impact of the maritime conditions, but remains conditioned by the oligotrophy of the soils.

Dynamic can be cyclical. A micro-patch of vegetation may reappear over time. Progressive dynamic of Retro-coastal heathlands are characterized by the appearance of preforest wooded species such as gorse (*Ulex europaeus* subsp. *europaeus*), blackthorn, pear, elm, oak. The relict heathland remains a refuge zone for heathers between separated patches of scrublands. Supply of litter, absence of light and transformation of the soil are unfavorable factors to Retro-coastal heathlands. However, changing climatic conditions, such as severe droughts or storms with high wind and salt spray deposition, can limit the development or even temporarily eliminate scrubs. Heather persists and can colonize bare or thin soils with *Agrostis capillaris*, *Agrostis curtisii* Kerguélen or *Festuca* spp. communities. Edge vegetation is favored by the dynamic transition diversity between scrublands, heathlands and grasslands. Edge forest species line the scrubs patches: *Teucrium scorodonia, Rubus* sp., *Polypodium interjectum,* etc.

We propose to consider five stages for the dynamic of Retro-coastal heathlands (Fig. 8):

- Stage -1: very open heathland dominated by grasses; it is either a phase of colonization of the heathers and gorses after destruction of the ligneous cover by fire, heavy grazing or other disturbances;
- Stage 0: "typical" Retro-coastal heathland, where some scrubs can occasionally appear;
- Stage 1: characterized by more frequent scrubs which replace heathers;
- Stage 2: scrubs are high and dominant;
- Stage 3: trees are dominant and heathland tends to disappear.

The two last stages are sometimes absent, due to restrictive edaphic or climatic maritime constraints.

These different stages can be useful to for detailed mapping and monitoring.

Nowadays, Retro-coastal heathlands are rarely exploited by agropastoral activities. Even reduced in small patches, they have a great importance for the conservation of heather species and their dispersal (Piessens et al. 2005).

The place of edge vegetation in the dynamics

The edge vegetation is a verge vegetation that makes a “transition both structurally and dynamically between open (bare or pelousar) and closed (scrub and preforest) environments” (Géhu 1999). It corresponds to a linear and sometimes fragmented vegetation. Edge vegetation conquers open environments and participates to the re-

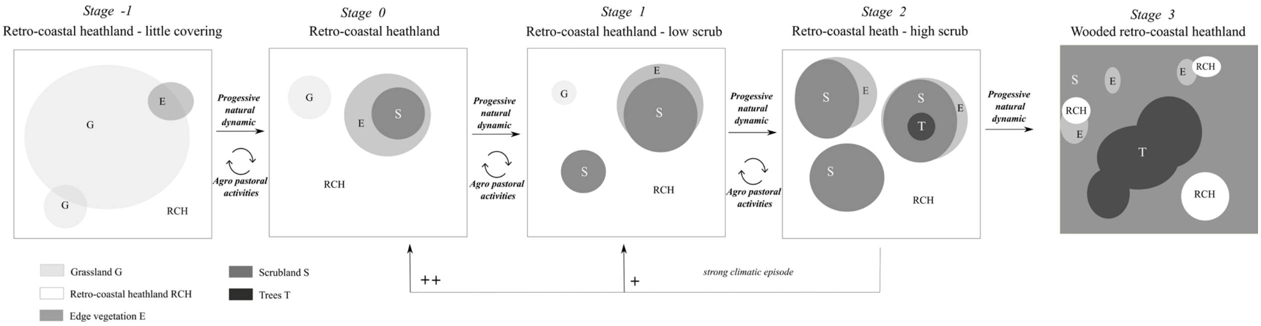

Figure 8. Dynamic of Retro-coastal heathlands: Progressive dynamic of colonization by patches of scrubs and trees and retrogressive dynamic following climatic episodes.

colonization processes of forests (Catteau 2012), species richness varies with the rapidity of dynamic evolution (Royer and Rameau 1981; Géhu 1999).

Coastal heathlands, which colonize bare soils, correspond to primary dynamics and concerns mainly stable maritime heathlands. In this case, no edge vegetation is observed.

We can consider that the presence of edge vegetation in coastal heathland landscapes characterizes secondary dynamics. It would represent the vestiges of a more wooded former vegetation.

In regressive dynamics, edge vegetation appears in dynamic contact with Retro-coastal heathlands. The presence of former wooded vegetation (scrubland, forest) is marked by the presence of forest relict species, which characterized edge vegetation.

On some coastal places, due to the abundance of livestock, overgrazing or soil trampling, appears a significant soil erosion. In the case of progressive secondary series, when the soils become too thin, edge vegetation species of the Retro-coastal heathland are rare or absent, ecological conditions do not allowing the development of a dynamic edge between the pioneer grassland and the heathland (Fig. 9).

Brachypodium rupestre communities

On the rocky cliffs of the Armorican Massif, edge vegetation with *Brachypodium rupestre* (Host) Roem. & Schult. (tor-grass) are present: *Teucrio scorodoniae-Brachypodietum rupestris* Bioret 2008, *Brachypodio rupestris-Peucedanetum officinalis* Bioret, N.Caillon & Glemarec 2014 (Royer 2016; Bioret et al. 2014). This species is also present in maritime grasslands: *Galio littoralis-Brachypodietum rupestris* (Géhu & Franck 1984) corr. Bioret 2008, *Anthyllido vulnerariae-Festucetum armoricanae* Bioret & Glemarec 2016 (Bioret and Glemarec 2016; Royer and Ferrez 2020) and *Festuco pruinosae-Brachypodietum rupestris* Arbesú, Bueno & F. Prieto 2002. This last association is located at the upper contact of the grasslands with

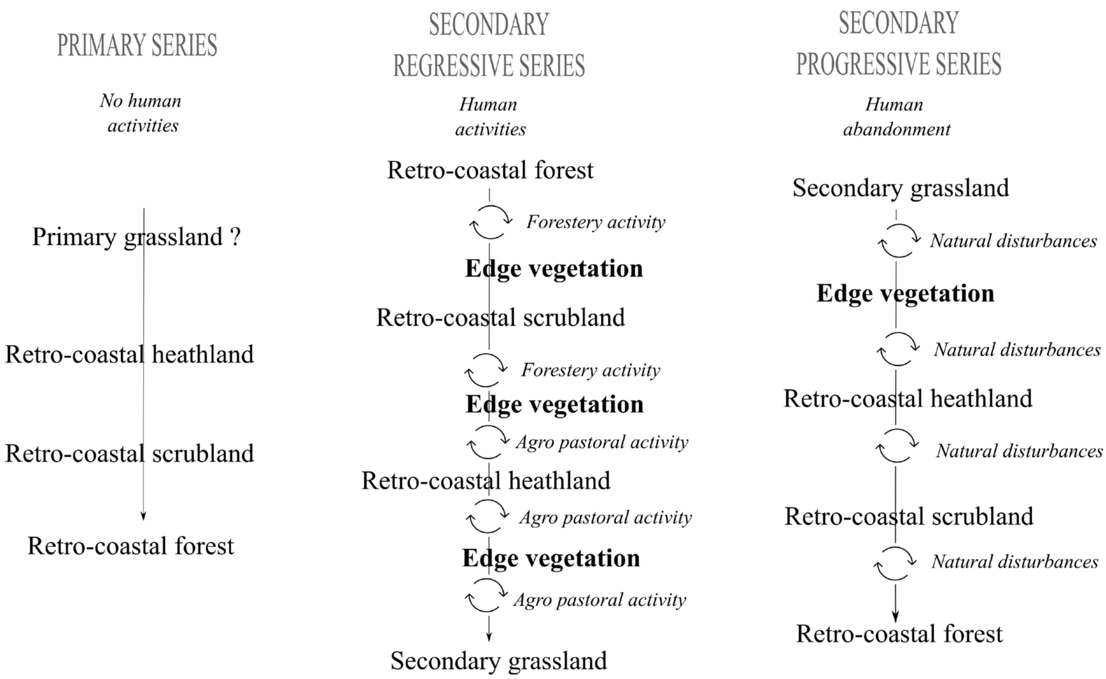

Figure 9. Place of edge vegetation in Retro-coastal heathlands secondary dynamic.

Festuca rubra subsp. *pruinosa*, considered as a serial stage towards coastal heathlands (Durán Gómez 2000).

On bedrocks releasing bases and mineral elements, such as dolerite (Cap Fréhel), micaschists (Belle-Île-en-mer) and rocky promontories with sandy shell soils (Cap d'Erquy), *Brachypodium rupestre* may occur in stable Medium sized maritime heathland. It characterizes phytosociological sub-associations of heathlands on calcic or magnesic soils, such as *Ulici humilis-Ericetum cinereae brachypodietosum rupestris* Géhu & Géhu-Franck 1975 and *Ulici maritimi-Ericetum cinereae brachypodietosum rupestris* Géhu & Géhu-Franck 1975 differentiated by *Brachypodium rupestre* and *Rosa spinosissima* L. subsp. *spinosissima* (Géhu and Géhu-Franck 1975). In this case, *Brachypodium rupestre* does not constitute patches of vegetation but is a simple component of the Medium sized maritime heathlands, mixed with heathers and gorses.

In other cases, *Brachypodium rupestre* vegetation occupies a larger area and constitutes a well-differentiated edge vegetation, in which heathland chamaephytes are rare and preforest species are present (*Hedera helix, Prunus spinosa, Rubia peregrina* L., *Teucrium scorodonia,* etc.); for example, *Teucrio scorodoniae-Brachypodietum rupestris*, on deep mesophilic soils of semi-sheltered coastal cliffs, in contact with maritime heathlands such as *Ulici maritimi-Ericetum vagantis* Géhu & Géhu-Franck 1975 (Bioret 2008), or *Brachypodio rupestris-Peucedanetum officinalis*, endemic to the dolerite veins of Cap Fréhel, which precedes a gorse scrubland. These plant communities constitute an edge vegetation associated to Medium sized maritime heathlands, maritime scrublands or Retro-coastal heathlands.

The presence of *Brachypodium rupestre*, which is not the expression of forest dynamics, characterizes former grazed abandonment landscapes. Vegetation is gradually invaded by this competitive species, with clonal multiplication (Rameau 1999). Density of *Brachypodium rupestre* seems proportional to the intensity of former grazing. This plant is also facilitated by fire, as a pyrophyte species (Rameau, *op. cit.*).

In summary, *Brachypodium rupestre* is observed in the Medium sized maritime heathlands on neutrocline soil. It can be scattered or abundant after grazing or fire. *Brachypodium rupestre* characterizes a scrub or forest dynamic only when associated with pre-forest species.

The dynamic place of *Prunus spinosa* scrublands

Prunus spinosa (blackthorn) scrublands are widespread over coastal cliffs. They are present in coastal heathlands landscape. They occupy deeper soils and can appear after heathlands in progressive dynamics. These scrubs constrained by environment and dynamically blocked, constitute minoriseries mature stage: *Ulici maritimi-Pruno spinosae minorisigmetum* (Demartini 2016). They can also represent dynamic stages towards a coastal forest.

Blackthorn can be related to Medium sized maritime heathlands, in mosaic, due to variability of soil conditions, or in dynamics. They can be present in suitable ecological conditions, completely independent of human action. *Prunus spinosa* scrublands can also be the remains of human uses such as agriculture, construction, quarries, etc.

Blackthorn's spreading can sometimes lead to the modification of micro-ecological conditions and the colonization of surrounding Medium sized maritime heathlands. In this case, cutting for ecological management or firewood, does not always leave place for heathland vegetation. However, its control by ecological management prevents propagation.

Environmental monitoring should be implemented to know if the Medium sized maritime heathlands can recover after *Prunus spinosa* scrublands cutting. Without mowing or grazing actions, blackthorn resprounting can arise rapidly.

Fig. 10 shows the dynamic place of *Prunus spinosa* and links with the Armorican cliff-top coastal heathlands.

Transgressive plant species

In primary dynamic successions, the colonization of bare spaces can be very variable due to the impossibility of predicting the dispersal capacity of the surrounding species and the influences of environment (van der Valk 1992). In the case of coastal cliffs, wind and salt spray deposition limit the possibility of soil colonization for plants, except halo-anemomorphic grasslands and heathlands species. However, once maritime heathland is established, occasional gaps linked to browsing by rabbits, agropastoral activity, seabird nesting, human-related erosion, etc. can appear. Some transgressive plant species, particularly fruit shrubs (brambles, blackthorns with seed dissemination by birds) or edge vegetation species (*Teucrium scorodonia, Dactylis glomerata, Brachypodium rupestre*) can, in an opportune moment, colonize primary stable maritime heathlands, by taking advantage of punctual disturbances. They are generally scattered, non-permanently established and do not reflect a real dynamic trend. Due to their autoecology, ligneous species are probably more self-sustaining than hemicryptophytes. For example, the maritime broom (*Cytisus scoparius* subsp. *maritimus*), which is a pioneer chamaephyte, is able to settle in a disturbed cliff-top heathland, and finally constitute a stable community (Glemarec and Bioret 2022). Annual or bisannual species can occupy bare spaces, but do not persist over time.

According to the plant strategies of Grime (1977), plants must adapt to three major environmental pressures: competition among themselves, habitat disturbance and stress. Pioneer or ruderal plants ("of early succession" in Hull et al. 2018) would be found mainly in disturbed and

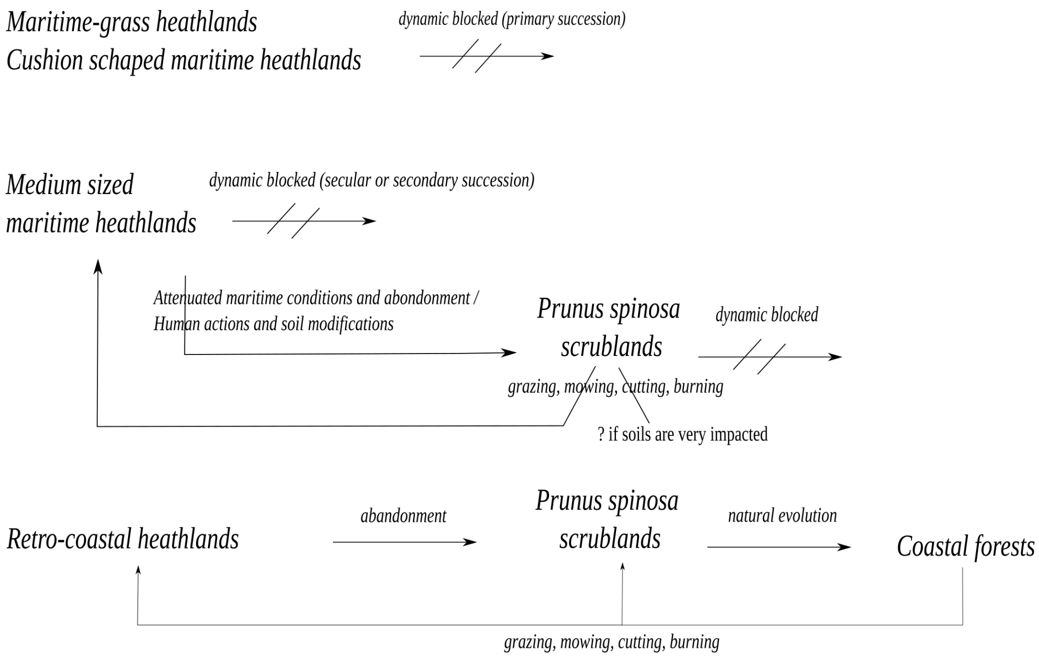

Figure 10. Dynamic place of *Prunus spinosa* scrublands in Armorican cliff-top coastal heathlands landscape.

low stress environments, where competition is low. For coastal cliffs, the stress due to wind and salt spray deposition is important, limiting the development of pioneer or opportunist species. They can be observed in disturbed soils (e.g. *Senecio jacobaea* Gaertn., *Cirsium vulgare* (Savi) Ten., *Senecio sylvaticus* L., *Urtica dioica* L., etc.). They can come from anthropized nearby places. Their occasional presence does not reflect the secondary character of the heathland. However their persistence reflects a change in environmental conditions and a modification of the ecological balance of the original heathland due to soil modification related to human disturbances (agriculture, quarries, old military constructions) or presence of animals (seabirds colonies or rabbit warrens).

In summary, maritime heathlands may occasionally integrate species from surrounding environments, due to little disturbances. Presence of brambles or blackthorn doesn't necessarily mean a dynamic to scrubland like Retro-coastal heathlands. It is therefore necessary to differentiate the punctual and non-lasting disturbance of a stable heathland and the progressive dynamics of an unstable heathland.

Hemeroby of coastal heathlands

Hemeroby is defined as the sum of the effects resulting from the anthropogenic impact on ecosystems. It is an integrative value taking into account human activities on ecosystems. Three dimensions are conditioning the effect of hemeroby: intensity, extent of exposure and duration of influence (Sukopp 1969). Hemeroby is the expression of artificial anthropic disturbances on vegetation (Kowarik 1990). As explained by Walz and Stein (2014) "in analysing current forms of land use in regard to human impact, hemeroby measures the distance between the current vegetation and a constructed final state of self-regulated vegetation in the complete absence of human intervention (so called potential natural vegetation (PNV))". The concept of "closeness to nature" promotes the original natural vegetation as a reference. Penas et al. (2005) propose a scale of vegetation naturalness (NI) based on the distance between the final phase of equilibrium (mature stage of the series) and its degree of anthropogenic influence or succession variation. These different concepts also describe naturalness. As written by Kim et al. (2002) "the highest level of naturalness is when the system has not been affected by man and is self-regulated". In the case of the most exposed maritime heathlands, the proximity to the sea and human access difficulty are correlated with a high rate of naturalness and a low level of hemeroby.

Coastal heathlands can be natural (primary succession with high maritime conditions) or semi-natural (secondary succession). They sometimes have been cultivated. If the plowing has been carried out at shallow depths, without main destructuration of the soil, heathlands may reappear (Chevrollier et al. 2021). In case of deeper plowing, heathlands disappear after modification of favorable edaphic conditions.

Regarding the resilience of heaths to fires, there is probably no difference between coastal and inland Armorican heathlands. After a running fire, inland heathlands regenerate, which is more rarely the case for humus fires (Clément 2008b).

Walz and Stein (2014) consider heathlands as "semi-natural mesohemerobic" vegetation. On coastal cliffs, "semi-natural mesohemerobic" vegetation correspond to secondary Medium sized maritime heathlands or Retro-coastal heathlands vegetation, which composition and structure testify former agro-pastoral uses as clearing and plowing, clean cutting, occasional light fertilization. Under strong maritime influences, Maritime grass-heathlands and Cushion shaped maritime heathlands could be consider, according to Walz and Stein scale as "natural ahemerobic" vegetation (no human impact) or a "oligohemerobic" vegetation close to natural (mowing, pastoralism).

According to Machado (2004), the main factors driving the naturalness are anthropic energies, anthropic elements and natural elements. Following Machado's evaluation grid, we consider that Maritime grass-heathlands and Cushion shaped maritimes characterize environments with a high value of naturalness ("virgin natural system" or "natural system"). Medium sized maritime heathlands and Retro-coastal heathlands are considered as "natural system" or "quasi or sub-natural system".

As synthesized by Loidi (2021), the hypothetical character in PNV (Loidi et al. 2010b) construction is the lower position of the community in the successional series (Zerbe 1998 in Loidi 2021) and the higher with high hemeroby; cliff slope vegetation could be "oligohemerobic" and cliff headland vegetation could be "mesohemerobic" (Fig. 11). We propose to consider heathlands from the top of the coastal cliffs as oligohemerobic vegetation, the past actions of grazing or fires remaining close to the natural pressures of large herbivores, climatic hazards, natural erosion. Some Maritime grass-heathlands and Cushion shaped maritime heathlands, located at the top of the cliffs, on outcropping rocks or stony soils, are close to the "ahemerobic" vegetation. When coastal heathlands have been subject of repeated mowing or cutting, without destruction of the landicolous soils, they must be considered as "mesohemerobic" vegetation, as well as for the Medium sized maritime heathlands whose dynamic mature stage is heathland or scrubland vegetation (it depends on the distance to the sea and the soil oligotrophy) or Retro-coastal heathlands, whose dynamics were blocked by human action.

Phytosociological checklist of Armorican cliff coastal heathlands

Several halo-anemomorphic ecotypes of the genus *Ulex* (*Ulex europaeus* subsp. *europaeus* f. *maritimus*, *Ulex gallii* subsp. *gallii* f. *humilis*, *Ulex latebracteatus* (Mariz) Rivas Mart., T.E.Díaz & Fern.Prieto f. *humilis*, *Ulex latebracteatus* subsp. *izcoi* Rivas Mart., Amigo & Pulgar f. *pulvinatus*), *Cytisus* (*Cytisus scoparius* subsp. *maritimus*) and *Genista* (*Genista pilosa* L. f. *maritima*, *Genista tinctoria* L. f. *prostrata* Corill., Figureau & Godeau) behave as differential taxa of different communities of cliff coastal heathlands in the Atlantic coast (Bridgewater 1980; Géhu 1975; Rivas-Martínez 1979; Glemarec et al. 2015).

In the Armorican Massif, cliff coastal heathlands communities can be differentiated and several plant associations have been described (Bioret 1994; Géhu 1963b; Géhu and Géhu-Franck 1975; Bioret and Davoust 2000; Géhu, 2000; Bioret and Géhu 2008; Guitton et al. 2018; Bioret et al. 2014). They are characterized by the presence of three *Fabacae* ecotypes: *Ulex europaeus* subsp. *europaeus* f. *maritimus*, *Ulex gallii* subsp. *gallii* f. *humilis* and *Cytisus scoparius* subsp. *maritimus*. The plant communities are presented according to the types of coastal heathlands. Distribution area and characteristic species are mentioned.

Maritime grass-heathlands:

- *Dauco gadecaei-Ericetum vagantis* Bioret, Géhu & Demartini 2014: Belle-Île-en-mer [*Erica vagans* L., *Daucus carota* subsp. *gadecaei* (Rouy & E.G.Camus) Heywood, *Plantago holosteum* Scop. var. *littoralis* (Rouy) Kerguélen, *Asparagus officinalis* L. subsp. *prostratus* (Dumort.) Corb., *Genista tinctoria* f. *prostrata*];
- *Festuco pruinosae-Callunetum vulgaris* Géhu 2000: Jersey [*Calluna vulgaris, Erica cinerea, Festuca rubra* subsp. *pruinosa*];

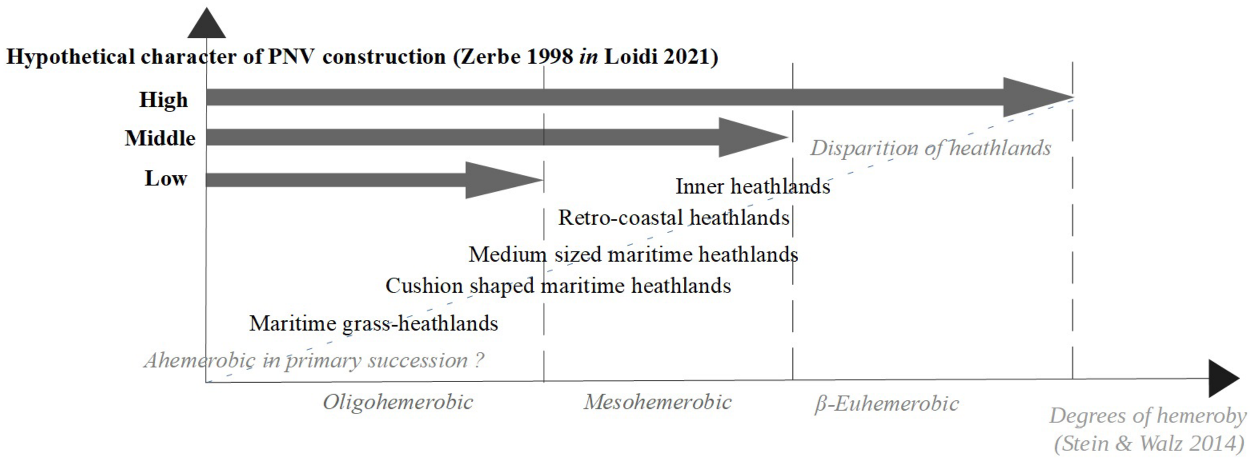

Figure 11. Hypothetical character of PNV construction and degrees of hemeroby of coastal heathlands [adapted from Loidi (2021)].

- *Festuca huonii-Erica cinerea* community: West Finistère [*Festuca huonii, Erica cinerea, Calluna vulgaris, Daucus carota* subsp. *gummifer*].

Cushion shaped maritime heathlands:
- *Scillo vernae-Ericetum cinereae* Bioret 1994: West Finistère [*Tractema* (syn. *Scilla*) *verna* (Huds.) Speta, *Erica cinerea*, *Calluna vulgaris, Solidago virgaurea* L. subsp. *rupicola* (Rouy) Lambinon];
- *Dactylido oceanicae-Cytisetum maritimi* Géhu 1963: West Finistère, Cotentin (Normandy) [*Cytisus scoparius* subsp. *maritimus*, *Erica cinerea*, *Dactylis glomerata* subsp. *oceanica*];
- *Festuco bigoudenensis-Ericetum cinereae* Bioret & Davoust 2000: Southwest Finistère [*Festuca ovina* subsp. *bigoudenensis* (syn. *Festuca guestfalica* subsp. *ophioliticola*), *Erica cinerea, Ulex europaeu*s subsp. *europaeus* f. *maritimus*];
- *Ulici maritimi-Ericetum cinereae* Géhu & Géhu-Franck 1975: Armorican Massif [*Erica cinerea, Ulex europaeus* subsp. *europaeus* f. *maritimus*] (Cushion shaped);
- *Ulici maritimi-Ericetum vagantis* Géhu & Géhu-Franck 1975: Belle-Île-en-mer and Groix islands [*Erica vagans, Ulex europaeus* subsp. *europaeus* f. *maritimus*] (Cushion shaped);
- *Ulici humilis-Ericetum cinereae* (Vanden Berghen 1958) Géhu & Géhu-Franck 1975: Armorican Massif, [*Erica cinerea, Ulex gallii* subsp. *gallii* f. *humilis*] (Cushion shaped).

Medium sized maritime heathlands:
- *Ulici maritimi-Ericetum cinereae* Géhu & Géhu-Franck 1975: Armorican Massif [*Erica cinerea, Ulex europaeus* subsp. *europaeus* f. *maritimus*];
- *Ulici maritimi-Ericetum vagantis* Géhu & Géhu-Franck 1975: Belle-Île-en-mer and Groix islands [*Erica vagans, Ulex europaeus* subsp. *europaeus* f. *maritimus*];
- *Ulici maritimi-Ericetum ciliaris* Wattez & Godeau ex Bioret & Géhu 2008: Loire-Atlantique [*Ulex europaeus* subsp. *europaeus* f. *maritimus*, *Erica ciliaris* L.];
- *Ulici humilis-Ericetum cinereae* (Vanden Berghen 1958) Géhu & Géhu-Franck 1975: Armorican Massif, [*Erica cinerea, Ulex gallii* subsp. *gallii* f. *humilis*]
- *Ulici humilis-Ericetum ciliaris* (Vanden Berghen 1958) Géhu & Géhu-Franck 1975: Armorican Massif, [*Erica ciliaris, Ulex gallii* subsp. *gallii* f. *humilis*];
- *Ulici humilis-Ericetum tetralicis* Bioret, N. Caillon & Glemarec 2014: Cap d'Erquy, Cap Fréhel (Côtes-d'Armor) [*Erica tetralix* L., *Ulex gallii* subsp. *gallii* f. *humilis*].

Retro-coastal heathlands:
- *Teucrium scorodonia-Erica cinerea* community: Armorican Massif [*Teucrium scorodonia, Erica cinerea, Rubus ulmifolius, Agrostis capillaris, Polypodium interjectum, Lonicera periclymenum*];
- *Erica cinerea-Erica vagans* community: Belle-Île-en-mer and Groix islands [*Erica vagans, Erica cinerea, Teucrium scorodonia*, *Ulex europaeus* subsp. *europaeus* f. *maritimus*, *Rosa spinosissima* subsp. *spinosissima*, *Cirsium filipendulum* Lange (Glemarec et al., 2019)];
- *Cisto salviifolii-Ericetum cinereae* Guitton, Juhel & Julve 2018: south of Vendée [*Cistus salviifolius* L., *Erica cinerea*].

Synphytosociological approach

The aim of synphytosociology is the study of the relationships between associations, from the pioneer ones to the climacic one, within a homogeneous ecological envelop corresponding to a *tessela* (Bioret et al. 2019). The different dynamic stages (mature, substitution, pioneering or anthropogenic vegetation) characterize the vegetation series (*sigmetum*), which is the fundamental unit of synphytosociology (Géhu 2006).

Permaseries (*permasigmetum*) is a permanent and stable plant community, little stratified and without stages of succession. This plant community represents both perennial vascular pioneer and maturity stages (Rivas-Martínez 2005; Lazare 2009). Minoriseries (*minorisigmetum*) is a vegetation series which does not present a forest mature stage, due to permanent ecological constraints (Rivas-Martínez et al. 2011). On coastal cliffs, minoriseries correspond to dense maritime scrubland or heathland which do not evolve towards higher scrubland or woodland.

Different ways of considering coastal Atlantic heathlands *geosigmeta* are developed by authors (Table 1). For Demartini et al. (2017), coastal Atlantic heathlands generally included in *minorigeosigmeta* (for example: *Ulici maritimi-Pruno spinosae geominorisigmetum*). At the lower contact, cliff rupicolous vegetation and halo-anemomorphic grasslands constitute a *geopermasigmetum*.

For Loidi (2021), coastal Atlantic heathlands are included in a coastal "halo-anemogenous rupicolous *geopermasigmetum*" where the permaseries are the vegetation belts arranged along the rock, depending on the inclination of the slope, the wind exposure and salinity gradients.

Salt spray deposition, containing mineral elements, is an important factor for cliff-top vegetation distribution (Malloch 1972; Chapman 1976; Gloaguen 1988; Sawtschuk 2010). Coastal cliffs characteristic species need salt spray deposition constraints to be more competitive than inland plants (Goldsmith 1973). The disappearance of halophilous species or the limitation of ecotypes can be considered as indicators of attenuation of salinity and wind constraints.

Heathlands permaseries occupy a strip in the upper edge of the cliffs depending on the sea influence intensity. The topography and the rocky soil are the other major factors determining the *catena* (homogeneous geomorphological envelop) (Géhu 2006), as it is related to the ability to build stable ground.

Table 1. Landscape phytosociological approaches of Atlantic cliff-top coastal heathlands .

Authors	Phytosociology	Synphytosociology	Geosynphytosociology
Demartini et al. (2017)	Coastal heathlands of *Dactylido oceanicae-Ulicion maritimi*	- mature stages of minoriseries - dynamic stage of coastal scrublands minoriseries	Geominoriseries
Lazare (2017)	*Smilaco asperae-Ericetum vagantis* (of Basque Corniche)	- subassociation as mature stage of a permaseries - subassociation as mature stage of a minoriseries - subassociation as dynamic stage of scrublands minoriseries	- Geopermaseries - Geominoriseries
Díaz González (2009) Loidi (2021)	Coastal heathlands of *Dactylido oceanicae-Ulicion maritimi*	Permaseries	Geopermaseries
Glemarec and Bioret (2023, in this article)	Coastal heathlands of *Dactylido oceanicae-Ulicion maritimi*: - Maritime grass-heathlands - Cushion shaped maritime heathlands - Medium sized maritime heathlands - Retro-coastal heathlands	- Permaseries: Maritime grass-heathlands, Cushion shaped heathlands, halophilic sub-associations of Medium sized maritime heathlands - Minoriseries whose mature stage is Medium sized maritime heathlands or maritime scrublands - Holoseries (coastal forests)	- Permaseries - Minoriseries - Holoseries

Lazare (2017) describes a coastal heathland, on the Basque Corniche cliffs, *Smilaco asperae-Ericetum vagantis* Lazare & Bioret *in* Lazare 2017. This coastal heathland presents three different dynamic trajectories therefore developed on three different juxtaposed *tessela*. The low-growing heathland (h = 25–30cm), *typicum* subassociation developed on rocky conditions, without herbaceous species, constitutes a halo-anemomorphic maritime rupicolous permaseries. The higher heathland (h = 50 cm), also belonging to the *typicum* subassociation, on thicker soils, where chamaephytes coexist with graminoid species, constitutes the terminal stage of a minoriseries. The third heathland corresponds to a second subassociation, *lathyretosum nudicaulis*, which evolves dynamically towards scrublands of *Rubo ulmifolii-Tametum communis* Tüxen in Tüxen & Oberdorfer 1958, constituting another minoriseries. In this example, the same subassociation, can represent both a permaseries (*Smilaco asperae-Erico vagantis typicum permasigmetum*) or a minoriseries (*Smilaco asperae-Erico vagantis typicum minorisigmetum*). The subassociation *lathyretosum nudicaulis* characterizes only a minoriseries (*Smilaco asperae-Erico vagantis lathyretosum nudicaulis minorisigmetum*).

The halo-anemomorphic grasslands of *Armerio maritimae-Festucetea pruinosae* Bioret & Géhu 2008 theoretically constitute permaseries. When observed in mosaic with *Ericaceae*, it is usually the influence of strong ecological constraints which blocks the establishment of a strict chamaephytic heathland. Several Armorican Cushion shaped maritime heathlands and Medium sized maritime heathlands present halophilous subassociations characterized by graminoid species such as *Festuca rubra* subsp. *pruinosa*. We propose to consider these halophilous sub-associations as permaseries.

Permaseries of Maritime grass-heathlands, Cushion shaped maritime heathlands and halophilic variations of Medium sized maritime heathlands
- *Scillo vernae-Erico cinereae permasigmetum*
- *Dauco gadecaei-Erico vagantis permasigmetum*
- *Festuco pruinosae-Calluno vulgaris permasigmetum*
- *Festuca huonii-Erica cinerea* community permaseries
- *Dactylido oceanicae-Cytiso maritimi permasigmetosum*
- *Ulici maritimi-Erico cinereae armerio maritimae permasigmetosum*
- *Ulici maritimi-Erico vagantis dauco gadeceai permasigmetosum*
- *Ulici humilis-Erico cinereae armerio maritimae permasigmetosum*

Minoriseries of *Medium sized maritime heathlands*
The primary and secondary grasslands remain to be studied with a phytosociological approach.
- *Festuco bigoudenensis-Erico cinereae minorisigmetum*
- *Ulici maritimi-Erico cinereae minorisigmetum*
- *Ulici maritimi-Erico vagantis minorisigmetum*
- *Ulici maritimi-Erico ciliaris minorisigmetum*
- *Ulici humilis-Erico cinereae minorisigmetum*
- *Ulici humilis-Erico ciliaris minorisigmetum*
- *Ulici humilis-Erico tetralicis minorisigmetum*

Figure 12. List of permaseries and minoriseries with a heathland as mature stage of the Armorican cliff-top coastal heathlands.

Table 2. Differentiation criteria of types of Armorican cliff-top coastal heathlands .

	1 Maritime grass-heathlands	2 Cushion shaped maritime heathlands	3 Medium sized heathlands	4 Retro-coastal heathlands
Abiotic factors				
Distance to the sea	<50m	<250m	<500m	<500m
Exposure to sea conditions	very exposed	very exposed	exposed	semi-sheltered
Major ecological constraints	maritime conditions and thin soils	maritime conditions	maritime conditions	thin and oligotrophic soils
Soil types	lithosoils or rankosoils	rankosoils soil thickness varies with rock type, deep soil possible on altered bedrocks with bases	rankosoils soil thickness varies with rock type, deep soil possible on altered bedrocks with bases	lithosoils or rankosoils
Biotic factors				
Hemeroby level / according to Walz and Stein (2014)	oligohemerobic	oligohemerobic	mesohemerobic	mesohemerobic
Ancient uses	possible extensive grazing	possible extensive grazing	soil sampling, extensive grazing, gorse harvesting, seaweed storage area	extensive grazing, cultivation with little impact on the soil (cereals, gorse), harvesting of gorse, harvesting of firewood
Actual uses	rare access for coastal fishermen	tourist visits, environment management	tourist visits, environment management	abandonment, urbanization
Physiognomy / Composition				
Vegetation structure	1 layer < 30cm	1 layer < 50 cm	50 cm < 1 layer < 100 cm	2 layers with high gorses or 1 layer > 100 cm
Physiognomy of gorses	very rare, always prostrated < 30 cm with necroses	gorses with cushion shape and some necroses < 50cm	gorses with medium sized and good vitality, rare necroses	moderately high (<60 cm), with forms in summit balls
Spatial homogeneity	homogeneous, with outcrops and halo-anemomorphic grasslands	homogeneous with gaps with bare ground	homogeneous	mosaic with scrubs and sparce coastal oak (elm) forest
Herbaceous, chamaephytic and phanerophytic cover	20% < herbaceous < 60% 20% < chamaephytic < 60 %	5 % < herbaceous < 10 % 60% < chamaephytic < 80 % (10 % < bare soil < 30 %)	5 % < herbaceous < 10 % 80% < chamaephytic < 100% 5% < phanerophytic < 10 %	5 % < herbaceous < 10 % 60% < chamaephytic < 90% 5% < phanerophytic < 40 %
Bionomic position				
Position on the zonation	Between halo-anemomorphic grasslands and maritime heathlands	Between halo-anemomorphic grasslands and Medium sized heathlands	Between halo-anemomorphic grasslands or Cushion shaped maritime heathlands and coastal forest series	Low maritime influence
Floristic composition				
Dominant genus taxa combination	*Festuca* + *Erica* + *Calluna*	*Calluna* + *Ulex*	*Erica* + *Ulex*	*Ulex* + *Erica* + *Teucrium* + *Rubus* + *Hedera*
Characteristic species	*Festuca huonii* *Festuca rubra* subsp. *pruinosa* *Calluna vulgaris* *Erica cinerea*	*Scilla verna* *Dactylis glomerata* subsp. *oceanica* *Calluna vulgaris* *Solidago virgaurea* subsp. *rupicola*	*Erica cinerea* *Ulex europaeus* subsp. *europaeus* f. *maritimus* *Ulex gallii* subsp. *gallii* f. *humilis*	*Teucrium scorodonia* *Polypodium interjectum* *Erica cinerea* *Hedera helix* *Ulex europaeus* subsp. *europaeus*
Syntaxa	*Dauco gadecaei-Ericetum vagantis* *Festuco pruinosae-Callunetum vulgaris* *Festuca huonii-Erica cinerea* community	*Scillo vernae-Ericetum cinereae* *Dactylido oceanicae-Cytisetum maritimi* *Festuco bigoudenensis-Ericetum cinereae* *Ulici maritimi-Ericetum cinereae* *Ulici maritimi-Ericetum vagantis* *Ulici humilis-Ericetum cinereae*	*Ulici maritimi-Ericetum cinereae* *Ulici maritimi-Ericetum vagantis* *Ulici maritimi-Ericetum ciliaris* *Ulici humilis-Ericetum cinereae* *Ulici humilis-Ericetum ciliaris* *Ulici humilis-Ericetum tetralicis*	*Teucrium scorodonia-Erica cinerea* community *Erica cinerea-Erica vagans* community *Cisto salviifolii-Ericetum cinereae*
Vegetation dynamics				
Type of succession	Primary succession	primary or secular succession?	secular succession (?), secondary	secondary

Table 2. Continuation.

	1 Maritime grass-heathlands	2 Cushion shaped maritime heathlands	3 Medium sized heathlands	4 Retro-coastal heathlands
Type of dynamics	blocked	blocked	blocked for halophilic variations, slow and progressive	slow and progressive
Progressive vegetation	-	-	*Ulici maritimi-Prunetum spinosae* Bioret et al. 1988	*Ulici maritimi-Prunetum spinosae* *Quercion roboris* Malcuit 1929 *Dryopterido affinis-Fraxinion excelsioris Bœuf et al. in Bœuf 2011*
Retrogressive vegetation	-	*Festucenion huonii* Bioret et al. 2014 (secondary) *Saginion maritimae* Westhoffet al. 1962	*Festucenion huonii* (secondary)	*Helianthemetea guttati* Rivas Goday & Rivas-Martínez 1963 *Melampyro-Holcetea mollis* Passarge 1994
Type of vegetation series	permaseries	permaseries	permaseries/minoriseries	minoriseries/holoseries
Vegetation expressing progressive dynamics	-	-	scrubs	scrubs, oak forest
Biomass production	+	+	++	+++
Size of the tessela (m²)	250	500	1000	500

The presence of unstable and very thin soil constraints the development of the coastal heathland. In the west and south of the Armorican Massif, these edaphic conditions favor the development of annual or perennial grasslands with *Festuca huonii*. Between these *Festuca huonii* grasslands and chamaephytic maritime heathlands on deeper soils, an ecological compartment often develops with intermediate edaphic conditions, stabilized by wind and salt spray deposition. These Maritime grass-heathlands with *Festuca huonii* (not in substitution place) and *Erica cinerea* or *Erica vagans*, without *Ulex*, (*Festuca huonii-Erica cinerea* community / *Dauco gadecaei-Ericetum vagantis*) also constitute permaseries.

When wind conditions are too strong for the installation of *Ulex*, herbaceous species are almost absent, and *Ericaceae* species are dominant, heather presents strong necrosis due to aridity and salt spray deposition. In this case, bare soil patches could be colonized by pioneer species, which do not indicate a progressive dynamic. These Cushion shaped maritime heathlands can be considered as permaseries.

We therefore propose to consider (Fig. 12) Maritime grass-heathlands, Cushion shaped maritime heathlands and the halophilic graminoid subassociations of the Medium sized maritime heathlands as permaseries. Medium sized maritime heathlands are the mature stages, or a dynamic stage, of minoriseries which final stage can be scrublands. Retro-coastal heathlands can constitute the mature stage of a secondary or a dynamic stage of series which mature stage can be coastal forest (holoseries).

European habitats correspondences

All Armorican cliff-top coastal heathlands belong to the Habitats 4030-European dry heaths and 4040-Dry Atlantic coastal heaths with *Erica vagans* (Annex I Directive habitats), which corresponding EUNIS codes are respectively F4.231 Maritime gorse heaths and F4.234 Northern *Erica vagans* heaths.

Retro-coastal heathlands can be considered as F4.235 Anglo-Armorican [*Erica cinerea-Ulex gallii*] heaths because these vegetation under hyper-Atlantic influences are located within the distribution area of *Ulex gallii*. On the southernmost coast of the Armorican Massif, some *Cistus* heathlands can occur, corresponding to habitat F4.24 Ibero-Atlantic *Erica-Ulex-Cistus* heaths.

According to Rodwell et al. (1991), British maritime heathlands can be grouped into the following communities: *Calluna-Scilla* heath (H7), which correspond according to our proposal to Maritime grass-heathlands or Cushion shaped maritime heathlands; *Erica vagans-Schoenus nigricans* heath (H5), *Erica vagans-Ulex europaeus* heath (H6) or *Calluna vulgaris-Ulex gallii* heath (H8) *Scilla verna* sub-community, which correspond to Medium sized maritime heathlands.

Armorican cliff-top coastal heathlands syntaxa and their European correspondences are presented in the appendix of this article.

Synthetic presentation of Armorican cliff-top coastal heathlands

The table 2 presents the different characteristics of the four types of cliff-top coastal heathlands, allowing their comparison and field determination. Transects presented in Fig. 13 show examples of distribution of coastal heathlands on Armorican cliffs in different situation of exposure and bed-rock.

For each type of heathlands, discriminant criteria are:

- *Abiotic factors*: climatic and physico-chemical factor independent of living beings;

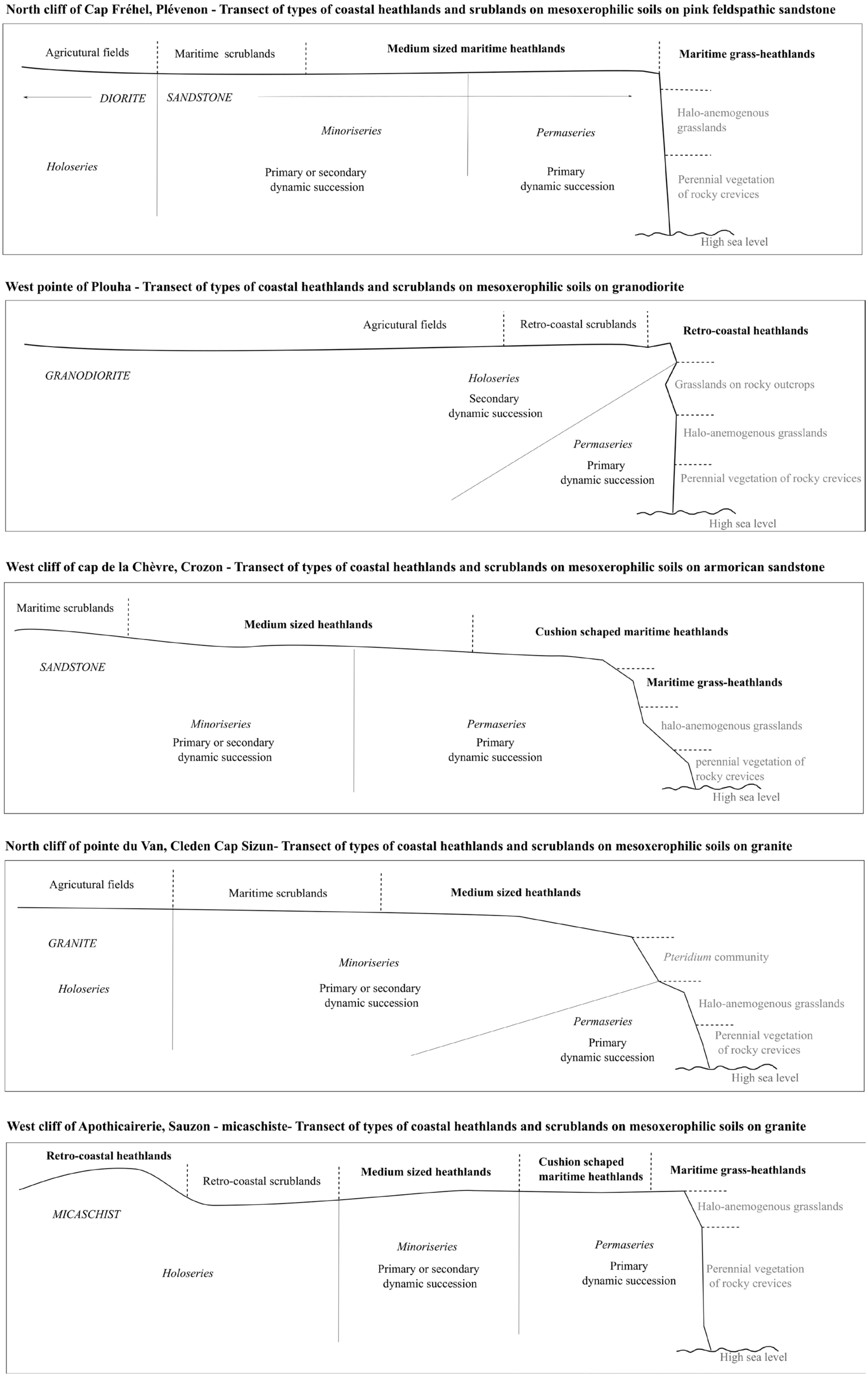

Figure 13. Examples of simplified transects of types of Armorican cliff-top coastal heathlands.

- *Biotic factors*: biological factor related to living beings, also includes human uses;
- *Physiognomy*: aspect of the vegetation according to the biological forms of these structuring plants;
- *Bionomic position*: position in the zonation;
- *Floristic composition*: characteristic species;
- *Vegetation dynamics*: dynamic trends, vegetation series types and associated syntaxa.

Conclusion

Armorican cliff-top coastal heathlands present particularities in their composition, structure and floristic dynamics that differentiate them from inland heathlands. Structure of vegetation is depending on dominant species and their adaptive capacities. Wind and salt spray deposition exposure, depth and type of soils and past uses (hemeroby) represent the main ecological factors, which variations in intensity can play a major role in species composition and structure of the different heathlands. Some Armorican cliff-top coastal heathlands are nonetheless primary and could constitute primitive communities, corresponding to the only stage in a halo-edaphoxerophilic dynamic series of vegetation. Other coastal heathlands are secondary, some blocked dynamically due to climatic conditions but especially soil related to past uses (plagioclimax), constituting "derived series". Others are clearly secondary, with potential or expressed dynamics; they constitute a stage of coastal minoriseries or holoseries.

We propose four types of cliff-top coastal heathlands: Maritime grass-heathlands, Cushion shaped maritime heathlands, Medium sized maritime heathlands and Retro-coastal heathlands, which are differentiated by their structure and their dynamics (Fig. 14).

This article proposes theoretical concepts of the dynamics of coastal heathlands, where hypotheses of natural syndynamics and synanthropization are proposed. Setting up long-term monitoring of coastal heathland including a synphytosociological approach, can allow a better understanding of dynamic links. Such monitoring cannot be undertaken without a historical ecology approach. Indeed, it must be supplemented by collecting historical data, allowing to answer to the primitive, secular or secondary character of the most maritime heathlands (anthracology – woodland clearance, ancient maps, ethnographic surveys, etc.) (Prøsch-Danielsen and Simonsen 2000; Savukyniene et al. 2003; Nilsen 2004; Robin et al. 2018; Glemarec and Bioret 2021). The whole constitutes a "research procedure" such as specified by Faliński (2003) including "methods for the collection of data (observational and experimental) and their mutual relations, the means by which the data are obtained and the data source can be verified, and the manner in which conclusions are drawn. The procedure is only successful if planned properly and pursued effectively to the benefits of both theoretical and practical ecology".

This research aims to contribute to the optimal conservation of these natural and semi-natural ecosystems by a better understanding of their mechanisms, necessary for

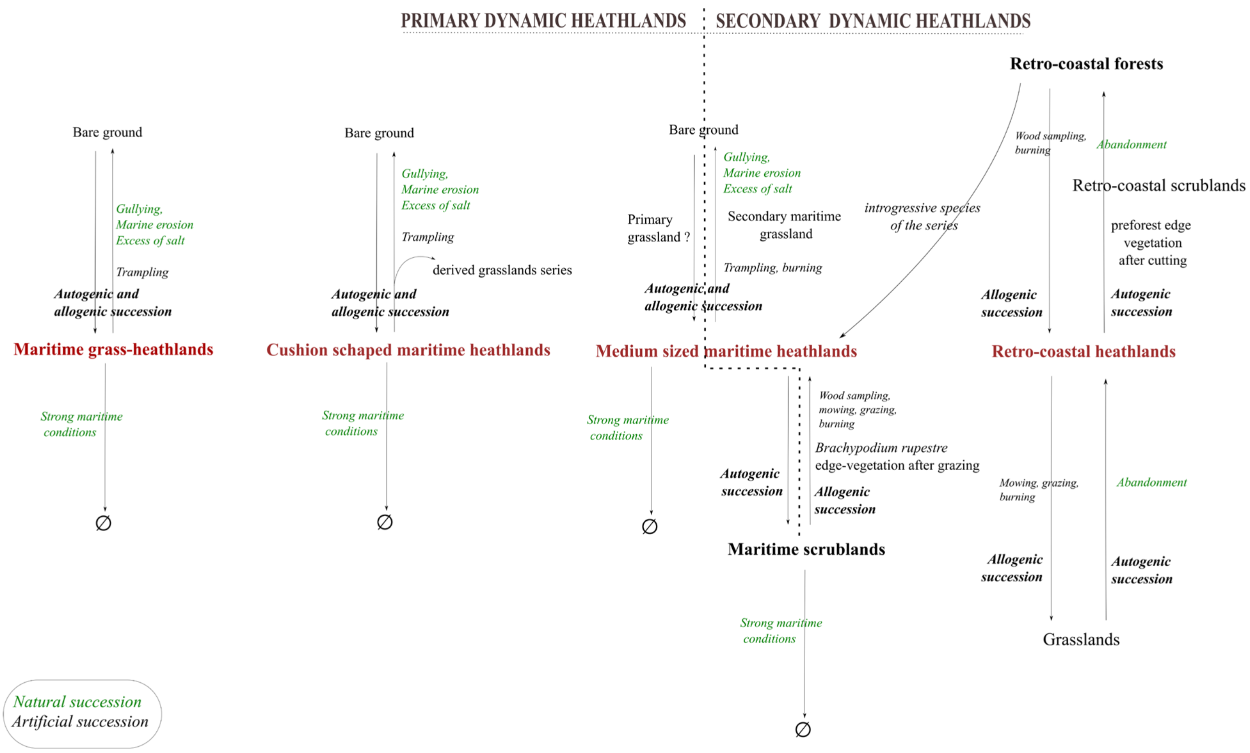

Figure 14. Dynamic scheme of Armorican cliff-top coastal heathlands.

decision-making for their conservative management, assessment of conservation status and long-term monitoring.

Knowing the possible dynamic of coastal heathlands according to the ecological conditions and the history of their uses by human is essential to drive the choice of environmental management: mechanical intervention, grazing or non-intervention, protection against erosion on frequented sites. The real issue is not only to determine the primary or secondary character of heathlands, but to understand their stability or instability, related to their capacity to produce biomass. The stress linked to maritime and soils conditions drive the productivity of plant communities. At the cliff site level, the issue of free dynamic of vegetation can be discussed, in order to maintain mosaics of different habitats.

At the European scale, this approach could be extended to the Atlantic coastal heathlands of Spain, Cornwall, Wales and Ireland. It could also concern heathlands on acidic or decalcified sands of non-rocky coastlines. The influence of tree plantations on the dynamic processes of coastal heathlands remains to be studied.

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Appendix I: Nature 2000 and Eunis correspondences of Armorican cliff-top coastal heathlands

Syntaxa	Habitat of Annex I Directive	French typology (Cahiers d'habitats Natura 2000)	EUNIS classification
Maritime grass-heathlands			
Dauco gadecaei-Ericetum vagantis	4040 Dry Atlantic coastal heaths	4040-1 Landes littorales thermophiles et atlantiques à Erica vagans	F4.234 Northern Erica vagans heaths
Festuco pruinosae-Callunetum vulgaris	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Festuca huonii-Erica cinerea community	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Cushion shaped maritime heathlands			
Scillo vernae-Ericetum cinereae	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Dactylido oceanicae-Cytisetum maritimi	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Festuco bigoudenensis-Ericetum cinereae	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Ulici maritimi-Ericetum cinereae - Cushion shaped	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Ulici maritimi-Ericetum vagantis - Cushion shaped	4040 Dry Atlantic coastal heaths	4040-1 Landes littorales thermophiles et atlantiques à Erica vagans	F4.234 Northern Erica vagans heaths
Ulici humilis-Ericetum cinereae - Cushion shaped	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Medium sized maritime heathlands			
Ulici maritimi-Ericetum cinereae	4030 European dry heaths	4030-2 Landes atlantiques littorales sur sol assez profond	F4.231 Maritime gorse heaths
Ulici maritimi-Ericetum vagantis	4040 Dry Atlantic coastal heaths	4040-1 Landes littorales thermophiles et atlantiques à Erica vagans	F4.234 Northern *Erica vagans* heaths
Ulici maritimi-Ericetum ciliaris	4030 European dry heaths	4030-2 Landes atlantiques littorales sur sol assez profond	F4.231 Maritime gorse heaths
Ulici humilis-Ericetum cinereae	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Ulici humilis-Ericetum ciliaris	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Ulici humilis-Ericetum tetralicis	4030 European dry heaths	4030-3 Landes atlantiques littorales sur sol squelettique	F4.231 Maritime gorse heaths
Retro-coastal heathlands			
Teucrium scorodonia-Erica cinerea community	4030 European dry heaths	4030-5 Landes hyperatlantiques subsèches	F4.235 Anglo-Armorican [*Erica cinerea* - *Ulex gallii*] heaths
Erica cinerea-Erica vagans community	4030 European dry heaths	4030-5 Landes hyperatlantiques subsèches	F4.235 Anglo-Armorican [*Erica cinerea* - *Ulex gallii*] heaths
Cisto salviifolii-Ericetum cinereae	4030 European dry heaths	4030-4 Landes sèches thermo-atlantiques	F4.24 Ibero-Atlantic *Erica* - *Ulex* - *Cistus* heaths.