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Impact of long-term drainage on the vegetation of an alpine raised bog: A case study of the Krumauer Moor (Austria)

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Christoph Muck BSc

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Abstract

Alpine raised bogs are highly sensitive to long-term drainage, which alters hydrological conditions, promotes peat decomposition and can shift vegetation towards forest-influenced states. This study assessed vegetation composition and structure in the Krumauer Moor (Austria), an alpine raised bog that has been subjected to approximately 60 years of drainage for forestry purposes and evaluated whether ecological indicator values can serve as proxies for restoration-relevant site conditions.

Vegetation was recorded in 1 x 1 m plots across three main site types: open bog (reference), bog forest (reference) and drained bog. Within the drained bog, mounts, former surfaces and drainage ditches were considered as distinct microfeatures. Two seasonal surveys (May and August) were pooled due to negligible seasonal differences. Environmental conditions were characterized by soil water content, peat decomposition (Von Post scale), soil pH and canopy density. Vegetation patterns were analyzed using community composition, dominance structure and indicator-based assessments, including separate indicator value calculations for bryophytes and vascular plants.

Species composition differed significantly among site types, with a clear multivariate separation between open bog, bog forest and drained bog plots. Drained bog vegetation was floristically closer to bog forest than to open bog vegetation, indicating a shift towards forest-influenced communities. Vegetation composition was strongly structured by gradients in water content, peat decomposition and canopy density. Typical raised bog species characterized the open bog, whereas drained conditions were associated with reduced peat-forming *Sphagnum* species and increased forest mosses and forest-related vascular plants. Microfeatures differed markedly: drainage ditches remained strongly *Sphagnum*-dominated and could still host typical raised bog vascular plants, while mounts represented the most degraded conditions.

Landolt indicator values provided robust proxies for moisture and light conditions, showing strong relationships with measured water content, peat decomposition and canopy density, but only limited correspondence with chemical site variables. Overall, the results highlight hydrological alteration as the primary driver of long-term vegetation change and support the use of vegetation-based moisture and light indicators as complementary tools for restoration-oriented site assessment in drained alpine raised bogs.

Kurzfassung

Alpine Hochmoore reagieren sehr empfindlich auf langfristige Entwässerung, die die hydrologischen Bedingungen verändert, die Torfzersetzung fördert und zu einer Vegetationsveränderung hin zu einem Waldzustand führen kann. Diese Studie untersuchte die Zusammensetzung und Struktur der Vegetation im Krumauer Moor (Österreich), einem alpinen Hochmoor, das seit etwa 60 Jahren für forstwirtschaftliche Zwecke entwässert wird, und bewertete, ob ökologische Indikatorwerte als Proxies für die für die Revitalisierung relevanten Standortbedingungen dienen können.

Die Vegetation wurde auf 1 x 1 m großen Parzellen in drei Hauptstandorttypen erfasst: offenes Moor (Referenz), Moorwald (Referenz) und entwässertes Moor. Innerhalb des entwässerten Moores wurden Aufschüttungen, ehemalige Oberflächen und Entwässerungsgräben als eigenständige Mikrofeatures betrachtet. Aufgrund vernachlässigbarer saisonaler Unterschiede wurden zwei saisonale Erhebungen (Mai und August) zusammengefasst. Die Umweltbedingungen wurden anhand des Bodenwassergehalts, der Torfzersetzung (Von-Post-Skala), des pH-Werts des Bodens und der Baumkronendichte charakterisiert. Die Vegetationsmuster wurden anhand der Zusammensetzung der Pflanzengemeinschaft, der Dominanzstruktur und indikatorbasierter Bewertungen analysiert, einschließlich separater Indikatorwertberechnungen für Bryophyten und Gefäßpflanzen.

Die Artenzusammensetzung unterschied sich deutlich zwischen den Standorttypen, wobei eine klare multivariate Trennung zwischen offenen Mooren, Moorwäldern und entwässerten Moorflächen zu beobachten war. Die Vegetation der entwässerten Moore war floristisch eher mit der Vegetation der Moorwälder als mit der der offenen Moore vergleichbar, was auf eine Verlagerung hin zu waldbeeinflussten Gemeinschaften hindeutet. Die Vegetationszusammensetzung war stark durch Gradienten im Wassergehalt, in der Torfzersetzung und in der Baumkronendichte strukturiert. Typische Hochmoorarten prägten das offene Moor, während entwässerte Bedingungen mit einer Verringerung der torfbildenden *Sphagnum*-Arten und einer Zunahme von Waldmoosen und waldbezogenen Gefäßpflanzen einhergingen. Die Mikrofeatures unterschieden sich deutlich: Entwässerungsgräben blieben stark von *Sphagnum* dominiert und konnten noch typische Hochmoor-Gefäßpflanzen beherbergen, während Aufschüttungen die am stärksten degradierten Bedingungen aufwiesen.

Die Landolt-Zeigerwerte lieferten robuste Proxies für Feuchtigkeits- und Lichtverhältnisse und zeigten eine starke Korrelation mit dem gemessenen Wassergehalt, der Torfzersetzung und der Baumkronendichte, jedoch nur eine begrenzte Übereinstimmung mit chemischen Standortvariablen. Insgesamt unterstreichen die Ergebnisse, dass hydrologische Veränderungen der Hauptfaktor für langfristige Vegetationsveränderungen sind, und sprechen für die Verwendung von vegetationsbasierten Feuchtigkeits- und

Lichtindikatoren als ergänzende Instrumente für die restaurationsorientierte Standortbewertung in entwässerten alpinen Hochmooren.

Table of contents

1. Introduction

Peatlands are among the most efficient terrestrial ecosystems for long-term carbon storage, yet they belong to the most heavily degraded ecosystems in Europe. Large areas of formerly intact peatlands have been drained for agriculture, forestry and peat extraction, resulting in profound and long-lasting alterations of their hydrology, biogeochemistry and vegetation (Bonn et al., 2016). In recent decades, however, a paradigm shift has occurred, and peatland conservation and restoration have increasingly become priorities within European environmental policy and climate strategies (European Commission, 2022). Recent meta-analyses and national restoration programs indicate a rapid increase in both the number and spatial extent of peatland restoration projects across Europe (Kustina et al., 2025; Laudon et al., 2025). This growing restoration effort highlights the urgent need for a sound understanding of long-term drainage impacts in order to support effective and ecologically meaningful restoration planning.

Vegetation plays a central role in the functioning of raised bog ecosystems, as peat formation and long-term carbon accumulation depend directly on the dominance of peat-forming plant communities, particularly *Sphagnum* mosses. Drainage primarily affects bog ecosystems through sustained lowering of the water table, which alters oxygen availability in the peat, accelerates peat decomposition and disrupts the positive feedback between *Sphagnum* growth and waterlogged conditions (Frankl & Schmeidl, 2000; Rydin & Jeglum, 2013). These hydrological changes subsequently trigger pronounced shifts in plant community composition and vegetation structure, favoring species adapted to drier and more aerated substrates and promoting successional pathways towards heathland, grass-dominated stages and, eventually, woodland communities (Talbot et al., 2010; Maanavilja et al., 2014; Haapalehto et al., 2017).

In Austria, most raised bogs have been affected by a long history of land use, including peat cutting and drainage for agricultural and silvicultural purposes. The Enns Valley in the central Eastern Alps represents a typical example of this development. Following deglaciation, extensive wetland complexes developed within the valley floor, but only small and fragmented remnants persist today, many of them in a degraded ecological condition. The remaining peatlands are now protected under national and European conservation legislation. This also applies to the Natura 2000 site “Pürgschachen-Moos und ennsnahe Bereiche zwischen Selzthal und dem Gesäuseeingang” (Land Steiermark, 2017), which includes the Krumauer Moor. In this area, parts of the formerly open raised bog were drained after the Second World War to facilitate the establishment of spruce plantations (Hasitschka, 2013).

While drainage-driven vegetation change in raised bogs has been widely documented in boreal and temperate lowland regions, particularly in peatlands drained for forestry (e.g.

Talbot et al., 2010; Maanavilja et al., 2014; Haapalehto et al., 2017), comparable long-term studies from alpine raised bog systems remain scarce. Differences in climate, growing season length and topographic context may influence both successional pathways and the persistence of typical bog vegetation under prolonged drainage. Consequently, it remains largely unclear to what extent vegetation trajectories described from boreal and lowland forestry-drained peatlands can be transferred to raised bogs of inner-alpine valleys.

Against this background, the ongoing revitalization planning for parts of the drained Krumauer Moor offers a unique opportunity to investigate long-term drainage effects on vegetation composition and site conditions in an upland raised bog in the alpine region. Understanding how plant communities respond to sustained drainage and peat decomposition is essential for identifying restoration priorities and for assessing the potential for the recovery of peat-forming vegetation.

The present study therefore addresses the following research question:

What changes have 60 years of drainage and peat decomposition caused to the vegetation composition and site conditions of an alpine upland raised bog site, and can ecological indicator values be used to estimate site parameters relevant for peatland revitalization?

Based on current conceptual models of drainage-induced vegetation change and successional pathways in raised bogs (Frankl & Schmeidl, 2000; Rydin & Jeglum, 2013; Talbot et al., 2010; Maanavilja et al., 2014), the following hypotheses are tested:

(1) The vegetation on drained bog areas shows a greater resemblance to transition or forest-influenced communities than to typical raised bog assemblages.

(2) With decreasing soil water content and increasing peat decomposition, both the richness and the cover of typical species for intact raised bogs decline.

(3) The cover of peat-forming *Sphagnum* species decreases with increasing drainage effects, while non-peat-forming bryophytes increase.

(4) Ecological indicator values of the vegetation can be used as proxies for site conditions relevant to revitalization; drained sites are expected to exhibit lower indicator values for moisture and light, and higher values for reaction and nutrients than intact bog sites.

2. Theoretical Background

Understanding the ecological functioning of raised bogs and their vegetation is essential for interpreting the patterns observed in the collected field data. The hydrological, chemical, and biological processes that shape ombrotrophic peatlands create highly specialized environmental conditions, which in turn determine vegetation structure, species composition, and ecosystem dynamics. Because these processes also respond sensitively to anthropogenic disturbance, in this context, especially drainage, this theoretical chapter provides the conceptual foundation required to analyze the vegetation, soil, and hydrological measurements obtained in this study.

By outlining the key characteristics of peatland ecology, plant functional groups, plant communities, and the mechanisms and consequences of degradation, the chapter establishes the framework necessary to contextualize the results and evaluate them within a restoration perspective.

2.1. Raised Bogs: Ecology, Hydrology, and Human Impact

Peatlands are globally significant wetland ecosystems characterized by the long-term accumulation of organic matter under waterlogged and oxygen-poor conditions. Through the suppression of aerobic decomposition, peatlands act as one of the most important natural carbon sinks, over the past 10,000 years they have sequestered an estimated 1.2 trillion tons of atmospheric CO_2 and today store approximately twice as much carbon as all the world's forests combined (Parish et al., 2008). Their ecological functioning is defined by a tight coupling between hydrology, nutrient availability, and the composition of specialized plant communities that can sustain peat formation. Compared with other wetland types, peatlands are extremely nutrient-poor and acidic, with surface water pH values often at or below 4 (Rydin & Jeglum, 2013).

Scientifically, peatlands can be defined in different ways. Pedological definitions emphasize the substrate, typically requiring the presence of a peat layer at least 30 cm thick and containing over 30% organic matter (Steiner, 1992). Ecological definitions instead focus on vegetation capable of producing and maintaining peat, which includes both the living plant communities and their degradation stages. A more integrative definition considers peatlands as wetland habitats with potentially peat-forming vegetation, underlain by peat or anmoor soils depending on site history (Schröck et al., 2022).

Despite these commonalities, peatlands encompass a wide range of hydrological conditions and nutrient regimes. A fundamental distinction exists between minerotrophic fens, which receive water enriched with dissolved minerals, and ombrotrophic bogs, which are fed exclusively by precipitation (Rydin & Jeglum, 2013). This difference in water supply creates distinct ecological contrasts. While fens may show substantial chemical heterogeneity, bogs are characterized by chemical uniformity, extreme oligotrophy, and strong acidity. Their strong dependence on precipitation also makes bogs highly sensitive to regional climatic conditions, leading to pronounced biogeographical patterns but relatively homogeneous conditions within a given region (Steiner, 1992; Dierßen & Dierßen, 2001).

Raised bogs represent, within the category of bogs, a specific ombrotrophic form distinguished by their characteristic convex surface. Unlike other peatland types, including fens and transitional mires, raised bogs maintain a surface elevated above the surrounding landscape (see Fig. 2.1). This elevation is supported by a thick peat body with extremely low hydraulic conductivity, which prevents lateral drainage and enables the development of an internal rain-fed groundwater mound (Rydin & Jeglum, 2013; Steiner, 1992). As a consequence, raised bogs are hydrologically isolated from surrounding mineral soils and depend entirely on atmospheric inputs for both water and nutrients, which explains their extreme nutrient limitation, high acidity, and ecological specialization (Rydin & Jeglum, 2013).

Raised bogs also exhibit distinctive microclimatic conditions. Because their large, largely immobile water mass buffers heat poorly, they experience extreme daily and seasonal temperature fluctuations, shortened growing seasons, and frequent ground frost even during summer months. These harsh conditions support a flora dominated by peat mosses (*Sphagnum* spp.) and a small set of adapted vascular plants, many of which are otherwise typical of subalpine or boreal environments. (Steiner, 1992)

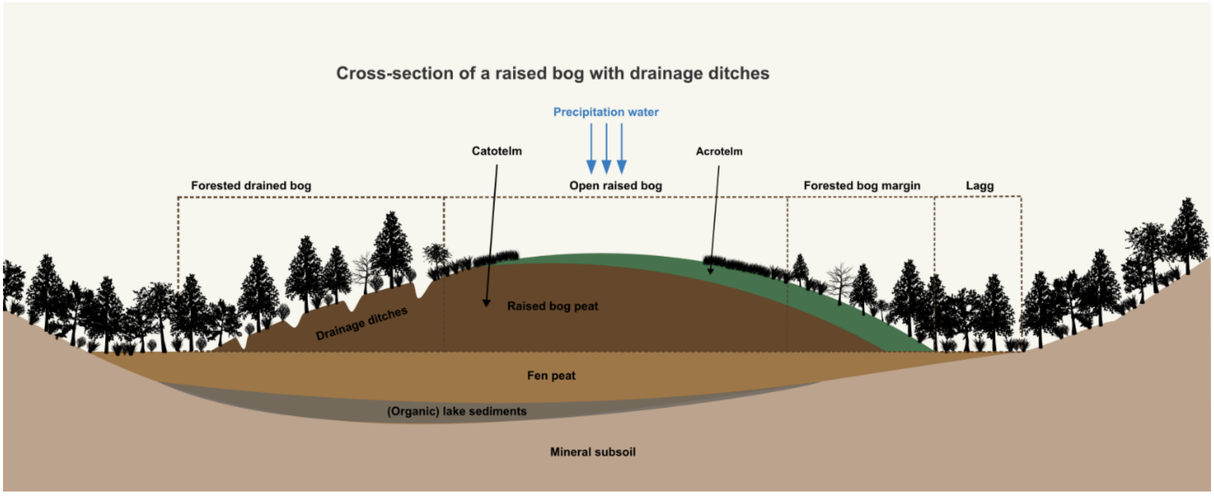

Figure 2.1: Schematic cross-section of a raised bog with drainage ditches, including sediment layers and a graphic representation of the dominant vegetation types (Own illustration)

A typical raised bog, as shown in Fig. 2.1, has a dome-shaped ridge that rises above the surrounding landscape. Since these bogs usually develop from fens, which in turn are formed by the silting up of water bodies, three types of sediments can be distinguished. Mineral or organic lake sediments lie directly on the mineral subsurface and are overlaid by fen peat. (Dierßen & Dierßen, 2001) Above this rises the permanently water-saturated dome consisting of raised bog peat, which forms the catotelm. This is overlaid by the acrotelm, which interacts with the environment and contains the ground water table.

(Steiner, 2005) While *Sphagnum*-dominated plant communities are dominant in the moderately inclined open raised bog, oxygen supply and nutrient mineralization increase with greater inclination towards the edges. This enables the establishment of forest communities composed of pine, spruce, and/or birch trees at the bog margins. At the edge of the raised bog, where bog water comes into contact with mineral soil water from the surrounding area, a comparatively ombrotrophic and less acidic lagg forms. (Dierßen & Dierßen, 2001; Steiner, 1992)
If a raised bog is drained with ditches (as shown in Fig. 2.1), water runoff from the acrotelm, and often also from the catotelm, is accelerated and the groundwater level is lowered. The resulting increase in oxygen supply and mineralization of the soil facilitates the colonization or reforestation by forest communities. (Jungmeier & Werner, 2004; Steiner, 2005)

2.1.1. Formation and development of raised bogs

Raised bogs develop through a long-term autogenic process in which persistent water saturation, low decomposition rates, and peat-forming vegetation gradually build a peat body that becomes elevated above its surroundings. Their formation begins in minerotrophic settings, typically as fens, where waterlogged, oxygen-poor conditions slow decomposition, enabling organic matter to accumulate as peat (Egger et al., 2025; Rydin & Jeglum, 2013). Over time, peat thickness increases to a point at which the rooting zone and living vegetation are decoupled from groundwater inputs. From this stage onward, the ecosystem becomes ombrotrophic; receiving water and nutrients exclusively from precipitation (Rydin & Jeglum, 2013). As ombrotrophy develops, the peat surface adopts a characteristic dome-shaped morphology (as depicted in Fig. 2.1), with the central bog surface rising above the margin. This dome is not formed by mineral sediment deposition but entirely by organic matter accumulation. Raised bogs are thus hydrologically isolated systems, distinguished from other peatland types by their exclusive reliance on atmospheric water inputs and their extreme nutrient limitation.

The continued upward growth of the peat surface is driven primarily by *Sphagnum* mosses, whose biomass production and poor decomposability facilitate rapid vertical peat accumulation. As *Sphagnum* builds waterlogged acrotelm peat, it increasingly insulates the peat mass from mineral substrates. The vegetation creates conditions favoring its own persistence, resulting in a positive eco-hydrological feedback. This fits the broader concept of water-mediated vegetation switches. (Frankl & Schmeidl, 2000) By retaining water in their hyaline cells and acidifying the substrate, *Sphagnum* species promote an environment in which competing vascular plants are disadvantaged, further reinforcing bog development (Steiner, 1992).

2.1.2. Hydrology, chemical characteristics and nutrient limitation

The hydrology of raised bogs, as an ombrotrophic system with no lateral groundwater input, is defined by their exclusive dependence on precipitation as the only water and nutrient source (Joosten & Clarke, 2002; Rydin & Jeglum, 2013). Building on the developmental principles outlined in section 2.1.1, hydrological processes determine whether peat accumulation can be sustained, whether the bog surface remains waterlogged, and how raised bogs respond to natural variability and human disturbance.

Because raised bogs receive water solely from rainfall, a positive long-term water balance is essential for their development and maintenance. High annual precipitation that exceeds evapotranspiration is therefore a prerequisite for growth of ombrotrophic peat (Dierßen & Dierßen, 2001; Steiner, 1992). Precipitation water is inherently nutrient-poor and slightly acidic, which shapes the chemical and ecological properties of raised bogs (Joosten & Clarke, 2002). Regions with insufficient rainfall or high evaporative demand cannot support sustained bog development.
The strong dependence on precipitation means that raised bogs are highly sensitive to even slight water-table reductions. Even minor hydrological imbalances, such climatic (drought) or anthropogenic (drainage, runoff diversion), rapidly affect *Sphagnum* vitality and surface moisture, initiating vegetation change long before structural peat layers are altered (Frankl & Schmeidl, 2000; Eigner, 2003).

Hydrological functioning is strongly controlled by the vertical structure of the peat body. The acrotelm (see Fig. 2.1) describes the 40 to up to 100 cm thick, oxygenated upper layer, that contains the fluctuating groundwater table and is comprised living and dead *Sphagnum* as well as the roots and rhizomes of the vascular plants. This layer acts as a dynamic regulator of water storage and flow. Its porous *Sphagnum*-dominated matrix transport and stores large quantities of rainwater, mediates seasonal fluctuations and ensures the supply of moisture to the layer beneath during drought. (Steiner, 2005; Steiner, 1992)
Below it, the catotelm (see Fig. 2.1) forms an often many meters-thick, permanently water-saturated, anoxic layer, containing most of the raised bog's mass. Consisting of tightly packed peat, it is hydrologically stable and nearly impermeable, ensuring persistent waterlogging that protects accumulated peat from decomposition and slows drainage through low hydraulic conductivity. This structure allows raised bogs to maintain high water tables even when the surface rises above surrounding terrain. (Steiner, 1992)

Evapotranspiration constitutes the dominant water loss pathway in intact raised bogs. Trees and shrubs, where present, may substantially increase transpiration rates and thereby lower the water table, particularly in bog margins or drained areas (Dierßen & Dierßen, 2001). Only minimal water escapes laterally, typically through diffuse seepage at the bog margin, thus this flux is small due to the low permeability of deeper peat.

Although raised bogs function as hydrological units, their wetness at the surface is not spatially uniform. Small-scale differences in elevation, storage capacity, and evapotranspiration create microtopographic moisture gradients, manifested as wet hollows and slightly drier hummocks. These patterns regulate the distribution of *Sphagnum* species and other vegetation. (Rydin & Jeglum, 2013)

Raised bogs are defined by their strong acidity, very low ionic strength, and severe nutrient limitation, which results directly from their ombrotrophic water supply. Because all incoming water is derived from precipitation rather than mineral-enriched groundwater, solute nutrient concentrations are very low and chemical conditions are remarkably uniform compared to minerotrophic peatlands (Joosten & Clarke, 2002; Rydin & Jeglum, 2013). This nutrient-poor, acidic environment fundamentally shapes vegetation composition and ecosystem processes.

A key chemical characteristic of raised bogs is their consistently low pH. Most ombrotrophic bog surfaces exhibit pH values below 4.2, although seasonal fluctuations and local variation within bogs can cause temporary increases (Rydin & Jeglum, 2013).
The essential plant nutrients that facilitate plant development are typically scarce from raised bogs. These nutrients are only introduced through atmospheric deposition and are rapidly converted and subsequently weakly mineralized under undisturbed conditions. Consequently, these systems exhibit limitations in nitrogen and phosphorus. Chemical conditions within a raised bog are not entirely homogeneous. Studies across bog slopes show that Ka, Ca, Mg, and other cations may vary slightly along microtopographic gradients and through seasonal shifts, although the overall ionic composition remains extremely low (Rydin & Jeglum 2013). These subtle variations are often linked to differences in vegetation, peat type, or small-scale hydrological flow, but do not alter the fundamentally ombrotrophic status of the system.
Anthropogenic nutrient inputs, such as increased atmospheric nitrogen deposition or dust inputs from surrounding areas and sulfur-containing precipitation, can have a negative impact on the nutrient-limited environment of raised bogs. These are linked to the spread of species that are not typical of bogs. (Jungmeier & Werner, 2004) Disturbances to the water balance, such as drainage, also alter nutrient availability. As the peat dries out, aerobic decomposition processes are enabled, leading to mineralization and thus to nutrient enrichment. (Eigner, 2003; Steiner, 2005)

The acidic and nutrient-poor conditions are reinforced by the unique biochemical properties of *Sphagnum* mosses. Through cation exchange, *Sphagnum* takes up base cations, such as calcium and magnesium, by releasing hydrogen ions into the surrounding water. This continuous process acidifies its surroundings and limits access to nutrients for potential competitors, contributing to the consistently low decomposition rates, the suppression of bacterial activity, and the dominance of mycorrhizal fungi in nutrient cycling. (Rydin & Jeglum, 2013; Steiner, 1992) As a result, only a small suite of highly specialized vascular plants can persist under such conditions.

2.1.3. Microtopography and ecological gradients

The surface of raised bogs is rarely uniform, instead, these peatlands develop a fine scaled, climatically and hydrologically controlled microrelief that reflects long-term interactions among vegetation, peat accumulation, and water dynamics. Microtopography emerges from the capacity of different *Sphagnum* species to retain water and maintain growth under varying moisture regimes, thereby initiating subtle but persistent differences in peat formation and decomposition. Once established, these microforms amplify themselves through positive feedback. Vegetation patterns influence local hydrology, which in turn reinforces the spatial distribution of species and the resulting surface structure. (Dierßen & Dierßen, 2001)

Across intact bogs, a characteristic sequence of microhabitats can be distinguished along the gradient of declining water availability, ranging from the wettest depressions to the drier elevated features (depicted in Fig. 2.2). Where mean water tables lie near or above the surface, peat remains saturated and decomposition is slow, favoring hydrophilic bryophytes. As the surface rises and aeration increases, peat decomposition intensifies, allowing vascular plants, such as dwarf shrubs, to establish.

At the lowest positions lie mud-bottoms and pools, mostly or constantly inundated with water levels averaging between 0 and 20 cm above the peat surface. These areas are largely devoid of vascular plants and are only sparsely covered by creeping bryophytes or remain as exposed peat.

Slightly elevated carpets occur, situated approximately 10 cm above the average water surface, while being occasionally flooded. They are dominated by strong bryophyte layers, consisting particularly of *Sphagnum*, with only few vascular plants. These carpets remain so soft that footprints persist for long periods.

Positioned around 20 cm above the mean water table are lawns, that consequently experience stronger seasonal fluctuations in water availability. Lawns support a structurally diverse bryophyte layer and a dense cover of graminoids whose rooting systems leading to firmness of the surface. The highest peat accumulation typically occurs on this horizon, since *Sphagnum* remains consistently within the capillary fringe.

The driest microforms are the hummocks, elevated about 20-50 cm above the lowest water levels and characterized by better-aerated peat. These conditions permit the growth of dwarf shrubs and hummock-forming *Sphagnum* species that sustain peat accumulation under comparatively dry conditions.

Often the more general term “hollow” is used to combine the microtopographic features from lawns to pools, in order to describe the depressions between hummocks. (Dierßen & Dierßen, 2001; Rydin & Jeglum, 2013).

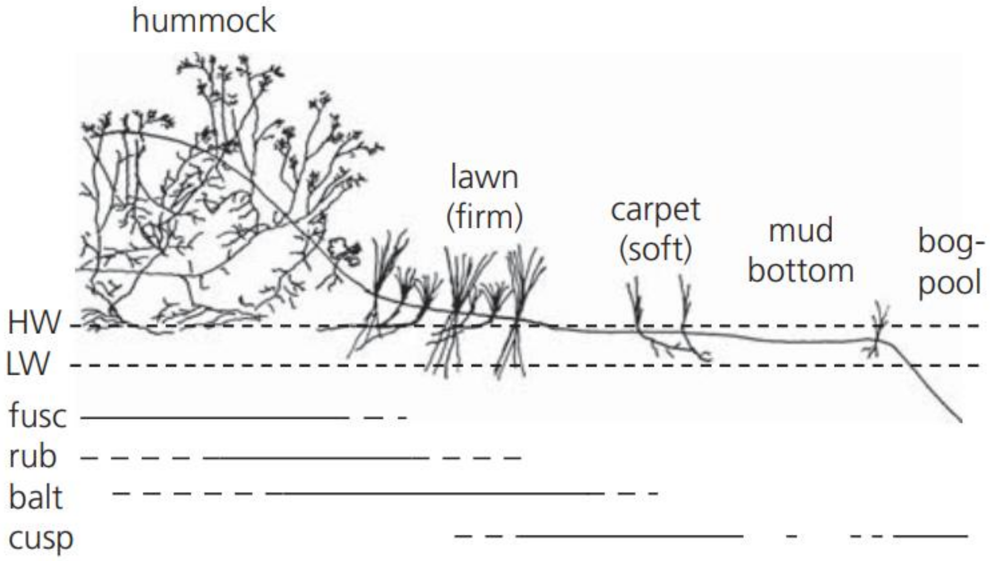

Figure 2.2: Illustration of the microtopographic gradient with associated vascular plant forms in a bog, also showing the estimated high (HW) and low water table (LW) and distribution of representative Sphagnum species (S. fuscum; S. rubellum; S. balticum and S. cuspidatum) (Source: Rydin & Jeglum, 2013)

2.1.4. Drainage of raised bogs: causes, mechanisms, ecological consequences

Drainage represents one of the most profound anthropogenic disturbances affecting raised bogs, fundamentally altering their hydrology, soil structure, vegetation and long-term stability. The primary motivations for drainage vary, ranging from attempts to improve agricultural productivity, facilitate forestry, or enable peat extraction. However, the underlying mechanism remains the same, lowering the water table within the acrotelm and, in severe cases, within the catotelm. This shifts the bog ecosystem away from its water-saturated condition and triggers a cascade of ecological changes. (Bonn et al., 2016; Haapalehto, 2014; Steiner, 1992; Steiner, 2005; Jungmeier & Werner, 2004)

Historically, bogs were drained to expand cultivable land or to increase the yield of surrounding agricultural areas. In many European regions, drainage was also implemented to enable afforestation, as conifers such as *Picea abies* and *Pinus sylvestris* were viewed as economically valuable but could not establish under natural bog hydrology (Jungmeier & Werner, 2004). Industrial peat extraction required even more extensive drainage networks, as both the acrotelm and catotelm needed to be dried to allow machine access and subsequent peat removal. Besides the direct drainage of raised bogs, the surrounding agricultural land is often drained in the immediate vicinity or within the lagg to improve land use. This practice can also reduce the height and stability of the bog's water mound. (Steiner, 2005)

Drainage disrupts the fundamental hydrological principle of raised bogs, with its reliance on a convex, rain-fed water mound formed by the extremely low hydraulic conductivity of the catotelm. When drainage ditches are cut into the bog surface, the acrotelm rapidly loses water to these artificial channels, and, if the ditches penetrate deeply enough, the catotelm can also become hydraulically connected to the drainage system (Steiner, 1992; Steiner, 2005). The hydraulic consequences extend far beyond the immediate ditch. According to the hydrological model described by Ingram and summarized in Steiner (1992), a drainage ditch effectively collapses a portion of the raised bog's water mound, causing a new, lower equilibrium surface to form on either side of the disturbance. If ditches are spaced too closely, these new equilibria may overlap, preventing the re-establishment of the original dome and resulting in irreversible hydrological degradation. Peripheral drainage can have equally severe effects. By lowering the external base level of groundwater, the entire raised bog mound may dry gradually, similar to a long-term climatic drying (Steiner, 2005).

Lowering the water table exposes previously water saturated peat to oxygen, which accelerates aerobic decomposition and the humifaction of *Sphagnum*-derived peat, leading to significant increases in nutrient concentrations (Haapalehto, 2014; Steiner, 2005). Enhanced decomposition of aerated peat results in substantial greenhouse gas emissions. On a global scale, drainage has turned many peatlands from carbon sinks into major carbon sources (Laudon et al., 2025; Parish et al., 2008).

Drying causes the peat to shrink through a reduction in pore volume and the rearrangement of soil particles, accelerating with increasing humification processes. This shrinkage is irreversible and even after rewetting, peat does not regain its former volume or hydraulic properties. As the catotelm loses its low water conduction capacity, overlying peat compacts further, degrading hydrological function and preventing uniform rewetting. (Steiner, 2005)

Lower water tables also facilitate changes in the structure of peatland ecosystems, as this enables deep-rooted vascular plants, especially birch, pine, spruce, and shrubs, to establish in previously treeless bog areas. Their rooting and high evapotranspiration reinforce local water level reduction and drive the shift from open bog vegetation toward bog woodland, marking a shift in plant community composition. (Haapalehto, 2014; Steiner, 2005; Jungmeier & Werner, 2004)

If drainage is severe, hydrological feedbacks may destabilize the entire system, causing the acrotelm-catotelm connection to break down, and the raised bog dome may collapse, preventing natural regeneration (Steiner, 1992).

2.1.5. Restoration of drained bogs: principles and approaches

The restoration of degraded raised bogs has become a priority in peatland conservation and climate mitigation, as drained peatlands represent one of the most significant anthropogenic sources of CO_2 emissions within the land-use sector. Because peat contains exceptionally high carbon densities, even partial degradation leads to disproportionately large greenhouse gas losses. Effective restoration is therefore essential not only for biodiversity but also for maintaining long-term carbon storage and hydrological function. (European Commission, 2022; Kustina et al., 2025; Laudon et al., 2025; Parish et al., 2008)

Across most temperate regions, drainage for forestry and agriculture has affected large portions of the peatland area (Bonn et al., 2016; Parish et al., 2008). Restoration strategies must therefore address the hydrological disruption that underlies nearly all degradation processes in raised bogs (Haapalehto, 2014). According to Eigner (2003), rewetting is the central and overriding measure in any restoration program, while all other interventions are secondary. The goal of rewetting is to raise the water table to near the ground surface in order to re-establish a functioning acrotelm. This requires the retention of oligotrophic rainwater, which is characteristic of natural ombrotrophic systems. Successful restoration depends on achieving a stable and consistently high water level, ideally without substantial seasonal drawdown. Overflooding, however, should be avoided to prevent excessive surface inundation that would hamper the re-establishment of bog vegetation. The most effective approach involves filling and compacting the entire ditch length, preferably with material excavated directly from the ditch. Crucially, this material should not be humified, because degraded peat no longer saturates properly and would not provide an effective hydraulic seal. (Eigner, 2003; Haapalehto, 2014)

Where degradation has not progressed too far, restoration of hydrology enables the return of natural vegetation, including peat-forming *Sphagnum* species, and can stimulate renewed carbon sequestration (Kustina et al., 2025; Parish et al., 2008). In such cases, rewetting restores the ecological feedbacks that maintain ombrotrophic conditions and can help prevent further carbon loss.

2.2. Vegetation of Raised Bogs

The vegetation of raised bogs is fundamentally shaped by the hydrological, chemical, and structural characteristics outlined in the previous chapter. As ombrotrophic systems, raised bogs are supplied exclusively by precipitation, resulting in persistently low pH and nutrient limitation (Rydin & Jeglum, 2013). These conditions create a uniquely selective environment in which only a small set of plants can persist, resulting in vegetation at these locations being similar worldwide and characterized by relative species poorness (Jungmeier & Werner, 2004). Because vegetation actively engineers the peatland environment, by regulating water storage, influencing decomposition, and driving peat accumulation, the composition and structure of plant communities are not merely passive responses to environmental constraints but central determinants of bog development and functioning. (Dierßen & Dierßen, 2001; Rydin & Jeglum, 2013)

The distribution of plant species and functional groups closely follows microtopographic gradients from hummocks to hollows, which reflect long term interactions between water table dynamics, the water-holding capacity of *Sphagnum* species, and differential peat accumulation (Dierßen & Dierßen, 2001; Rydin & Jeglum, 2013). These vegetation-controlled microforms in turn reinforce hydrological feedbacks that maintain the characteristic structure of raised bogs and support ecological differentiation over very small spatial scales.

Understanding the vegetation of raised bogs is therefore essential for interpreting both natural ecological patterns and anthropogenic impacts. Drainage, for instance, alters hydrology and microtopography in ways that shift vegetation composition, typically reducing *Sphagnum* cover and promoting graminoids, shrubs, and trees, thereby weakening peat accumulation and potentially destabilizing the bog's ecological integrity. (Parish et al., 2008; Rydin & Jeglum, 2013; Steiner, 2005) Conversely, restoration efforts aim to reverse these vegetation shifts by reinstating high water levels and reconstructing conditions favorable for peat-forming mosses (Eigner, 2003; Parish et al., 2008).

In the following sections, the major plant groups characteristic of raised bogs are examined in detail, beginning with bryophytes, particularly *Sphagnum* mosses, the principal drivers of peat formation, followed by other mosses, vascular plant groups, and the resulting plant communities. Finally, the chapter contextualizes these vegetation patterns within the framework of FFH habitat types and discusses the ecological responses of bog vegetation to drainage and succession.

2.2.1. Bryophytes

Bryophytes form the structural and functional foundation of raised bog ecosystems. Mosses dominate the ground layer because they tolerate prolonged saturation, low pH, and microclimatic conditions better than vascular plants (Steiner, 1992; Rydin & Jeglum, 2013). They drive many of the key ecosystem processes that define raised bogs: they retain large amounts of water, regulate moisture dynamics at the surface, and shape the microtopography that characterizes intact bogs (Dierßen & Dierßen, 2001).

Through their slow decomposition under persistently saturated, oxygen-poor conditions, bryophytes, especially *Sphagnum* mosses, accumulate to form peat. Their differential growth responses to water-table fluctuations create distinct microhabitats such as hummocks and hollows, each associated with characteristic plant assemblages and ecological conditions (Rydin & Jeglum, 2013; Dierßen & Dierßen, 2001). In this way, bryophytes are not only shaped by the hydrology of bogs but also actively maintain and reinforce it.

2.2.1.1. Sphagnum mosses

Sphagnum mosses are the ecological engineers of raised bogs and the primary drivers of peat accumulation. Their exceptional water-holding capacity and unique anatomical features allow them to dominate environments that are too acidic, nutrient-poor, and hydrologically unstable for most vascular plants. The large hyaline cells characteristic of the genus *Sphagnum* act as capillary reservoirs that can absorb and retain water amounting to more than twenty times their dry weight, while capillary transport enables rapid uptake and redistribution of precipitation water across the growing surface. (Steiner, 1992) Through these mechanisms, *Sphagnum* maintains a persistently wet acrotelm, stabilizing the high water tables required for peat formation (Steiner, 2005).

Equally central is the ion-exchange capacity of *Sphagnum* mosses, which allows them to replace cations from rainwater with hydrogen ions. This acidification further suppresses microbial activity and therefore limits nutrient availability, reinforcing the competitive dominance of *Sphagnum* over vascular plants and sustaining the characteristically low pH of bog surfaces. (Steiner, 1992) As decomposition is strongly inhibited under these acidic and waterlogged conditions, the dead biomass is pressed downward into permanently saturated layers, contributing to the formation of structurally distinct acrotelm and later catotelm peat (Steiner, 2005).
The length growth of the genus *Sphagnum* exhibits synchrony between individual peat moss plants, with this growth occurring in the shoot sections immediately below the head. The increase in length ranges from about 1 to 10 cm per year, varying between species and locations. The apical branches of the peat moss heads exhibit primary photosynthetic activity. Long-day conditions and higher temperatures enhance photosynthetic performance when there is sufficient water supply, while short-day conditions and low temperatures reduce it. (Dierßen & Dierßen, 2001)

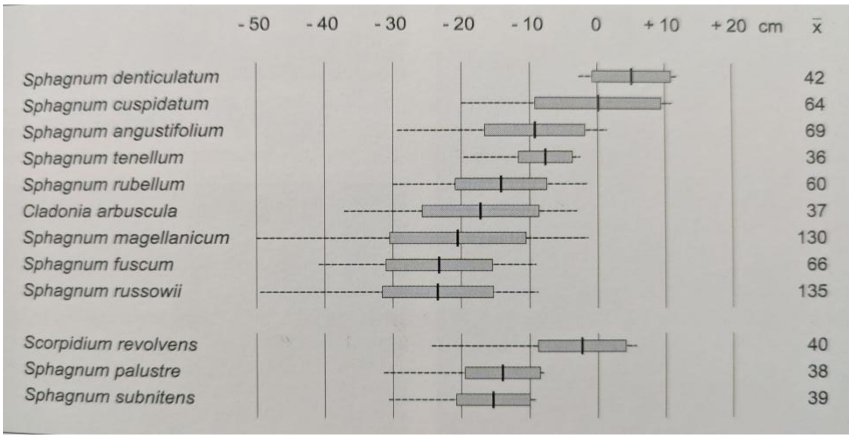

Figure 2.3: Hydrological niches of common moss and lichen species in Black Forest moors (Germany). The bars show water levels in relation to the surface of the individuals studied. x = number of measurements (Source: Dierßen & Dierßen, 2001)

As depicted in Fig. 2.3, different *Sphagnum* species occupy specific water-table positions and thereby shape the microtopography of raised bogs. Species tolerant of wetter microhabitats, such as *S. cuspidatum* or *S. angustifolium,* form lawns to mud-bottom communities, whereas taxa more affine to drier and aerated conditions, like *S. magellanicum* and *S. capillifolium*, build hummocks elevated well above the average water table (Rydin & Jeglum, 2013; Dierßen & Dierßen, 2001). These zonations emerge from species-specific growth rates, water retention capacities, and competitive relationships and form the basis for the characteristic hummock-hollow complex evident in intact bogs (Fig. 2.2).

2.2.1.2. Other bryophytes

Beyond the clearly dominant *Sphagnum* mosses, raised bogs and their transition zones are home to a diverse but ecologically subordinate collection of other mosses, whose occurrence is strongly structured by pronounced hydrological gradients. Their distribution reflects moisture availability, shading, microtopography, and disturbance history, and changes in their abundance often indicate ecological changes, particularly drainage and succession. (Rydin & Jeglum, 2013)

Along the microtopographic gradient, Dierßen & Dierßen (2001) describe a transition from carpet-forming liverworts and mosses in the wettest microforms to feathermoss-dominated assemblages on the driest hummock crests. While *Sphagnum* species dominate peat formation across most microforms, non-*Sphagnum* bryophytes increasingly appear where conditions become less saturated and more aerated. On dry hummock tops, especially in slightly elevated or wooded bog areas, *Pleurozium schreberi* and *Hylocomium splendens* form characteristic mats, replacing peat-forming *Sphagnum* and indicating low water tables and increased shading (Dierßen & Dierßen, 2001; Rydin & Jeglum, 2013). It should also be noted here that, in addition to bryophytes, lichens of the genus *Cladonia* can also occur on dry hummocks (Dierßen & Dierßen, 2001).

Feathermosses (*Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis*) are particularly indicative of treed bogs and drained sites, where reduced water levels, greater aeration, and canopy cover create microclimatic conditions similar to moist coniferous forests. Their expansion is therefore a widely recognized sign of hydrological alteration or successional change (Rydin & Jeglum, 2013).
Other bryophyte species such as *Aulacomnium palustre, Dicranum spp.* and *Polytrichum spp.*, colonize exposed or disturbed peat surfaces. These species often occur after drainage, peat cutting, or physical disturbance, and may temporarily dominate regenerating surfaces before *Sphagnum* re-establishes (Rydin & Jeglum, 2013). Their presence therefore frequently reflects early successional stages or anthropogenic impact.

In the following, all of the bryophyte species described in this chapter will be classified under the term "forest mosses," despite the fact that some of these species are also typical of the open raised bog. This categorization is implemented to facilitate the distinction between *Sphagnum* and other bryophyte species.

2.2.1.3. Peat-forming vs. non-peat-forming mosses

For the interpretation of vegetation patterns and drainage effects in raised bogs, it is essential to distinguish between moss species that contribute substantially to peat accumulation and those that do not. Peat formation in ombrotrophic bogs is almost exclusively driven by *Sphagnum* species. According to Rydin & Jeglum (2013), all three sections of the genus *Sphagnum, Acutifolia*, *Sphagnum* and *Cuspidata* form specific peat types, depending on peatland type and their morphology. But the bulk of *Sphagnum* peat worldwide seems originate from species belonging to the sections *Acutifolia* and *Sphagnum*. The previously described morphological and physiological traits, such as hyaline water-storage cells, upward growth with burial of older tissues, and strong acidification capacity, enable long-term organic matter accumulation under waterlogged conditions. These traits make *Sphagnum* the principal peat-forming group in raised bogs.

Other bryophytes that often occur in bogs, including feathermosses (*Pleurozium schreberi*, *Hylocomium splendens*) or species such as *Aulacomnium palustre*, differ markedly in their contribution to peat formation. Feathermosses typically occupy the driest hummock surfaces or drained sites, where their biomass decomposes rapidly and does not persist in the peat profile. *Aulacomnium palustre* can contribute to peat accumulation under certain conditions, particularly in disturbed or regenerating peat surfaces, but its peat is less characteristic, more decomposed, and forms much more slowly than that derived from *Sphagnum*. (Bauer et al., 2007, Rydin & Jeglum, 2013)

Consequently, *Sphagnum* species are the only species considered to play a primary role in the formation of peat in this particular context. While forest moss species can also contribute to peat formation under specific conditions, their overall significance is minimal. The presence of these conditions necessary for peat formation cannot be determined.

2.2.2. Vascular plant groups

Vascular plants form an essential but comparatively small component of the vegetation in open raised bogs but increase in richness and dominance towards the bog margins or disturbed sites, reflecting the change in nutrient availability, acidic conditions, and hydrology (Dierßen & Dierßen, 2001; Rydin & Jeglum, 2013). Their distribution in intact open bogs follows the microtopographic and hydrological gradients outlined in Chapter 2.1.4., and they often serve as indicators of moisture regime, successional stage, and disturbance history. In contrast, forested bogs support a vascular flora shaped more strongly by shading, lowered water tables, and the expansion of woody species. (Dierßen & Dierßen, 2001; Steiner 2005)

Graminoids form the most visible group in wet to moderately moist microhabitats. In near-saturated hollows and low hummocks, sedges and rush-like species such as *Carex limosa*, *Carex rostrata*, and *Rhynchospora alba* dominate, often together with *Eriophorum vaginatum* and *Molinia caerulea* on slightly drier carpets and lawns (Dierßen & Dierßen 2001; Steiner 2005). Their strong root systems stabilize soft surfaces and contribute to the firmness of lawn communities described in Rydin & Jeglum (2013). These species are particularly characteristic of relatively open, undisturbed bog surfaces and decline when the water table drops and when shrub and tree cover increases.

Herbaceous species are generally sparse in ombrotrophic bogs, limited by the low nutrient availability and acidity. In wet hollows and lawns for example, the carnivorous *Drosera spp.*, and *Scheuchzeria palustris* and various sedges occur, often together with *Eriophorum vaginatum* (Steiner 2005). Towards wooded bogs an increase in species richness can be observed, indicative of gradual nutrient enrichment and enhanced aeration. (Dierßen & Dierßen, 2001; Rydin & Jeglum, 2013)

Shrubs, especially ericaceous dwarf shrubs, increase in importance with rising microrelief and towards the bog margins. On carpets formed by *Sphagnum magellanicum* and *S. angustifolium* small shrubs, like *Vaccinium oxycoccos* and *Andromeda polifolia* are prominent, while lawns to elevated hummocks also support larger species such as

Vaccinium vitis-idaea, *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Calluna vulgaris* and *Pinus mugo*, often together with *Sphagnum capillifolium* in Austrian bogs (Steiner 2005). These species generally tolerate the drier, more aerated conditions of higher microforms and are often more closely associated with hummocks then with lawns or even carpets (Dierßen & Dierßen 2001). The ericaceous shrubs found in raised bogs have developed adaptations that allow them to thrive in acidic and nutrient-poor environments. These adaptations include mycorrhizal associations, which facilitate nutrient acquisition, and sclerophyllous leaves, which enhance drought resilience. Therefore, these dwarf shrubs are able to expand in coverage under drainage or prolonged lowering of the water table, contributing to the transition from open bog to woody bog stages. (Rydin & Jeglum, 2013)

Trees are naturally rare in intact raised bog interiors but may establish along margins or on elevated hummocks. A limited number of species, *including Pinus sylvestris, Pinus mugo, Picea abies*, and *Betula pubescens*, exhibit the capacity to withstand the acidic, waterlogged conditions characteristic of these environments. (Rydin & Jeglum, 2013) According to Steiner (2005), the most elevated hummocks in raised bogs are frequently colonized by *Pinus sylvestris* or *Picea abies*, often accompanied by a ground layer of forest mosses. In areas where bogs have been drained or have undergone degradation, the presence of trees becomes increasingly prevalent. These trees invade former open areas or are deliberately planted, forming bog woodlands. The growth of these trees is facilitated by factors such as aerated peat, reduced water tables, and increased nutrient availability in the degraded peat. Once established, these trees promote further drainage of the root zones through strong transpiration in the crowns. (Dierßen & Dierßen, 2001; Rydin & Jeglum, 2013)

2.2.3. Plant Communities and Syntaxonomy of Austrian Raised Bogs

The classification of vegetation in this chapter follows the Central European phytosociological system of Braun-Blanquet as applied by Steiner (1992) in his comprehensive survey of Austrian peatlands. In this framework, plant communities are arranged hierarchically into classes, orders, alliances, and associations, each defined by characteristic species compositions and uniform ecological conditions.
Associations represent the fundamental units, defined as plant communities with a floristically well-defined composition and a uniform physiognomy that occupy habitats with consistent environmental conditions. Several associations with similar floristic structure form an alliance, alliances aggregate into orders, and orders into broad classes. Species fulfilling specific diagnostic roles are distinguished accordingly: character species are largely restricted to a given syntaxon and define it floristically; differential species separate closely related units within the same hierarchy; and companion species occur more broadly but contribute to the physiognomy of the community.
The subsequent section delineates the plant communities relevant to this study, providing concise descriptions of the class, order, and alliance. This is followed by a detailed characterization of the most important associations.

2.2.3.1 Dwarf shrub-dominated communities in moderately wet, acidic bog sites (Oxycocco-Sphagnetea)

Class: *Oxycocco-Sphagnetea* BRAUN-BLANQUET & TÜXEN 1943

Key species: Vaccinium oxycoccos, Eriophorum vaginatum, Andromeda polifolia, Drosera rotundifolia, Sphagnum magellanicum, S. capillifolium, S. tenellum, Mylia anomala, Cephalozia connivens

This class comprises the vegetation of hummocks and carpet zones of oligotrophic, acidic, predominantly ombrotrophic raised bogs across the Northern Hemisphere. Communities are floristically uniform due to the extreme nutrient limitation and dominance of peat-forming *Sphagnum* species. However, the class incorporates a variety of structurally distinct vegetation units, contingent on regional climate and hydrology. These include carpets comprising graminoids, hummocks supporting dwarf shrubs, and loose, multi-layered forest communities containing the characteristic species inventory. (Steiner, 1992)

Order: *Sphagnetalia magellanici* KÄSTNER & FLÖSSNER 1933 (PAWL. 1928)

Key species: Vaccinium oxycoccos, Vaccinium uliginosum, Eriophorum vaginatum, Andromeda polifolia, Carex pauciflora, Sphagnum magellanicum, S. capillifolium, S. fuscum, Polytrichum strictum, Calypogeia sphagnicola, Ledum palustre, Vaccinium vitis-idaea, Sphagnum russowii.

This order includes *Sphagnum*-dominated, often dwarf-shrub-rich vegetation of different oligotrophic bog types, transition mires but also acidic-oligotroph fens in the boreal and temperate zones. In Austria, it encompasses both drier open raised bog microforms and bog woodland units where species of the Oxycocco-Sphagnetea still dominate the understory. (Steiner, 1992)

Alliance: *Sphagnion magellanici* KÄSTNER & FLÖSSNER 1933 (MALC. 1929)

Key species: Vaccinium oxycoccos, Pinus mugo agg., Sphagnum magellanicum, S. capillifolium, Polytrichum strictum.

This alliance comprises the raised bog hummock communities of the temperate, subcontinental to continental zone in Europe. In Austria, Steiner (1992) recognized four associations, of which two are further described here:

Association 1: *Sphagnetum magellanici* KÄSTNER & FLÖSSNER 1933 (MALC. 1929)

The *Sphagnetum magellanici* represents a largely treeless association of raised and transitional bogs in the middle and higher elevations of the Central European mountains. Although it lacks true character species in the strict Braun-Blanquet sense, the community is floristically well defined through a distinctive combination of differential species, most notably *Sphagnum magellanicum*, *S. capillifolium*, *S. angustifolium*,

Polytrichum strictum, *Dicranum undulatum*, *Eriophorum vaginatum*, *Carex pauciflora*, *Vaccinium oxycoccos*, *V. uliginosum*, *Andromeda polifolia*, and *Drosera rotundifolia*.
Within the *Sphagnion magellanici*, it is distinguished from the other alliances and associations primarily by the absence of the typical diagnostic species *Ledum palustre*, *Trichophorum cespitosum*, and *Pinus mugo*, all of which characterize related bog communities on somewhat drier or climatically different sites. As a result, *Sphagnetum magellanici* forms the typical open raised-bog vegetation in many Austrian peatlands, with a physiognomy dominated by *Sphagnum* hummocks, ericaceous dwarf shrubs, and oligotrophic graminoids.
Although fundamentally ombrotrophic and therefore nutrient-poor, the association can be influenced locally by mineral-soil water inputs. In such settings, *Picea abies* may encroach. Even on strictly ombrotrophic sites, isolated, stunted spruces may also form a particular physiognomic variant often referred to as *spruce bog*. However, even where spruce occurs, shading remains minimal, the sparse, open canopy does not significantly modify light availability, humidity, or the species composition of the moss and dwarf-shrub layers. Consequently, these *Picea abies*-influenced stands represent structural variations rather than distinct syntaxonomic units. (Steiner, 1992)

Association 2: *Pino mugo-Sphagnetum magellanici* KÄSTNER & FLÖSSNER 1933 (NEUHÄUSL 1969 CORR.)

The *Pino mugo-Sphagnetum magellanici* represents the dwarf-pine (*Pinus mugo* agg.) bog association of the temperate mountain regions. It occurs on drier hummock sites of raised bogs, typically constantly elevated above the mean water table, where *Pinus mugo spp.* can establish alongside the characteristic species of the *Sphagnion magellanici*. Floristically, the association is defined by the presence of *Pinus mugo* together with typical oligotrophic bog species, including *Sphagnum magellanicum*, *S. capillifolium*, *Polytrichum strictum*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*, *V. uliginosum*, *Andromeda polifolia* and *Drosera rotundifolia*.
Structurally, the stands are shaped by the various forms within the *Pinus mugo* aggregate, which differ in growth habit but share similar ecological requirements. *P. mugo* s.str. typically forms low, around 2 m high, multi-stemmed aggregates; *P. rotundata* forms somewhat taller, more open stands mostly limited to the Austrian bohemian mass; and *P. uncinata* reaches only the westernmost regions, locally forming taller bog-pine stands.
The association occupies the drier portions of raised bogs, forming the woody counterpart within the *Sphagnion magellanici*. Despite the presence of *Pinus mugo spp.*, the vegetation remains *Sphagnum*-dominated, with hummock-forming species such as *S. magellanicum* or *S. angustifolium* maintaining the strongly acidic, nutrient-poor conditions typical of ombrotrophic peat. In some places, especially where slight minerotrophic influence occurs, *Picea abies* may appear within the association, but its shading effect remains limited and does not alter the characteristic composition. (Steiner, 1992)

2.2.3.2 Dwarf shrub-rich coniferous forests (Vaccinio-Piceetea)

Class: *Vaccinio-Piceetea* BRAUN-BLANQUET 1939

Key species: Vaccinium myrtillus, Vaccinium vitis-idaea, Pleurozium schreberi, Hylocomium splendens, Dicranum scoparium.

This class encompasses a broad spectrum of communities worldwide, including the dwarf shrub-rich coniferous forest communities in the boreal zone and mountains, as well as the dwarf shrub communities in the subalpine zone, birch forests in the boreal zone, and birch swamp forests. (Steiner, 1992)

Order: *Vaccinio-Piceetalia* BRAUN-BLANQUET 1939 em. KIELLAND-LUND 1967

Key species: Picea abies, Trientalis europaea, Dicranum majus, Ptilium crista-castrensis, Barbilophozia barbata, Lycopodium annotinum.

This order contains meso- to eutrophic coniferous forest communities. Along with the *Cladonio-Vaccinietalia* (oligotrophic dwarf shrub and coniferous forest communities), this is the only order relevant to Austria bog landscapes, typically occupying weakly minerotrophic margins, functioning as transitional units between bog and mineral-soil forests. (Steiner, 1992)

Alliance: *Vaccinio-Piceion* BRAUN-BLANQUET 1939 em. KIELLAND-LUND 1967

This alliance includes dwarf-shrub-rich spruce forests, hosting the same key species.

Association: *Bazzanio-Piceetum* BRAUN-BLANQUET 1939

The *Bazzanio-Piceetum* represents the spruce-dominated mire-margin forest community that typically forms transition zones around raised bogs, occurring on dry peat or anmoor soils. Floristically, it is characterized by *Picea abies*, *Bazzania trilobata*, *Sphagnum girgensohnii*, and *Dicranum scoparium*, with *Picea abies* and *Dicranum scoparium* functioning as differential species within the mire-forest context. The association develops where hydrological influence from the bog is reduced, creating a structurally distinct belt between ombrotrophic bog vegetation and mineral-soil coniferous forests.
Steiner (1992) distinguishes two main subunits based on substrate conditions and *Sphagnum* dominance, each of which contains characteristic variants.

The typical subunit corresponds to stands that develop on anmoor or raw-humus soils, often at a notable distance from the actual bog. In these locations, the typical variant forms a transitional belt that mediates between peatland and mineral-soil spruce forests, while the *Sphagnum palustre* variant, developing in moister microsites, such as drainage ditches or small depressions. Here, *Sphagnum palustre* becomes the dominant peat moss, accompanied regularly by *Sphagnum squarrosum*.
The subunit of *Sphagnum magellanicum* represents stands in which the *Bazzanio-Piceetum* transitions toward the spruce-dominated expression of the *Sphagnetum*

magellanici. These stands occur on peat substrates closer to the bog margin and are characterized by denser and taller spruce canopies than those found in the open bog woodland. In this more shaded environment, the *Sphagnum* layer becomes patchy, reflecting the reduced light availability and altered moisture regime. This subunit can be further divided into four distinct variants, each distinguished solely by the predominant *Sphagnum* species present. These species include *S. magellanicum, S. capillifolium, S. angustifolium,* and *S. fallax*. (Steiner, 1992)

2.2.4. FFH habitat types

The Natura 2000 habitat types represent standardized units used across the European Union to classify ecosystems of conservation importance. Raised bogs and bog woodlands are among these protected types, and only a subset is relevant to the study area. Based on the report for the Natura 2000 site "Pürgschachen Moos und ennsnahe Bereiche zwischen Selzthal und dem Gesäuseeingang" by the Moorschutzverein Pürgschachen (2005), the habitat types present within the Krumauer Moor are 7110 (active raised bogs), 7120 (degraded raised bogs still capable of natural regeneration), and 91D0 (bog woodland). The following overview summarizes their defining features, typical vegetation, and local occurrence.

2.2.4.1. 7110 - Active Raised Bogs

Active raised bogs ombrotrophic peatlands sustained primarily by nutrient-poor precipitation water. Their surface typically lies above the surrounding water table, allowing the development of characteristic microtopography such as hummocks, hollows, bog pools, and lagg zones. "Active" indicates the presence of vegetation that is normally peat-forming.

These habitats are strictly protected due to their exceptional ecological and historical value. As these habitats represent millennia-old, extremely nutrient-poor ecosystems, they host a suite of highly specialized plant species that are tightly bound to their acidic and oligotrophic conditions. Moreover, because organic material in the peat body does not decompose under the prevailing anoxic and acidic environment, these bogs serve as long-term archives of past environmental and vegetation history. (European Commission, 2013; LUBW, 2021a)

Vegetation is dominated by typical oligotrophic bog specialists. Characteristic plant species include *Sphagnum spp., Eriophorum vaginatum, Carex pauciflora, Andromeda polifolia, Vaccinium oxycoccos*, *Vaccinium uliginosum,* and *Drosera rotundifolia*. The habitat is floristically characterized by communities from alliances of *Sphagnion magellanici, Rhynchosporion albae*, and *Sphagno-Utricularion*.

Despite minor tree encroachment by *Pinus mugo spp.* or scattered spruce, the overall structure remains open and hummock-dominated. (Ellmauer & Traxler, 2001; LUBW, 2021a)

In the study region, intact raised bog vegetation persists only in very small areas. According to Moorschutzverein Pürgschachen (2005), the Krumauer Moor contains 1.0 ha of fragmented 7110 habitat, representing the last remnants of largely ombrotrophic communities.

2.2.4.2. 7120 - Degraded raised bogs still capable of natural regeneration

Habitat type 7120 comprises raised bogs whose natural hydrology has been disturbed, typically through drainage or peat cutting, leading to drying and shifts in species composition. However, ecological conditions still allow hydrological restoration and the re-establishment of peat-forming vegetation within an estimated timeframe of around 30 years. These habitats have a high conservation value due to their restoration potential and their importance as refuges for bog species in landscapes where intact bogs have become rare. (European Commission, 2013; LUBW, 2021b)

The vegetation reflects transitional and early successional states. Characteristic species include *Calluna vulgaris, Salix aurita, Frangula alnus, Betula pubescens, Picea abies, Pinus mugo ssp., Molinia caerulea*, alongside the active raised bog species *Sphagnum spp., Eriophorum vaginatum, Vaccinium oxycoccos and uliginosum, Andromeda polifolia, Drosera rotundifolia, Carex limosa*, and *Rhynchospora alba*.

Typical vegetation units include early succession stages of *Rhynchosporion albae, Sphagnion magellanici, Sphagno-Utricularion*, and components of *Salicion cinereae* or initial stages of *Piceo-Vaccinienion*. Compared to 7110, the microtopography is less pronounced, tree and shrub encroachment more widespread, and *Molinia caerulea* often becomes abundant. (Ellmauer & Traxler, 2001; LUBW, 2021b)

Across the study area, large parts of the former raised bog surfaces in the Krumauer Moor are classified as 7120 (Moorschutzverein Pürgschachen, 2005). These zones represent moor-degradation stages but maintain sufficient structural and hydrological potential to be restored to active raised bog (7110).

2.2.4.3. 91D0 - Bog woodland

Bog woodland comprises coniferous or mixed forests growing on wet, nutrient-poor peat, with water levels at or above the surrounding groundwater table. These woodlands occur on the margins of raised bogs, transition mires, or acid fens, and may also form loose stands extending across the bog surface.

Bog woodland can develop naturally under stable high-water conditions, but it may also arise secondarily where peatlands were degraded and subsequently colonized by trees. While such secondary bog woodland is included in 91D0, restoration measures may favor the re-establishment of open bog types (7110). Despite this, intact bog woodland supports characteristic *Sphagnum*-rich vegetation and represents an important structural component of the regional mire landscape. (European Commission, 2013; LUBW, 2021c)

Typical tree species include *Betula pubescens, Picea abies, Pinus sylvestris, and Pinus mugo spp.*. The field and ground layer usually contain *Sphagnum spp., Vaccinium uliginosum, Vaccinium oxycoccos, Vaccinium myrtillus, Calluna vulagris, Molinia* *caerulea, Andromeda polifolia*, as well as sedges such as *Carex canescens, Carex echinata*, and *Carex rostrata*.

Syntaxonomically, bog woodland in Central Europe corresponds to coniferous and broad-leaved forest communities of the *Vaccinio-Piceetea* and includes several characteristic associations already described for the region, such as *Bazzanio-Piceetum* and *Pino mugo-Sphagnetum magellanici*. Depending on hydrology and peat depth, these forests may occur as birch bog woods, pine bog woods, or spruce-dominated mire forests. (Ellmauer & Traxler, 2001; LUBW, 2021c)

In the Krumauer Moor, bog woodlands have developed on the edge of raised bogs and transition bogs on wet peat substrate, under oligotrophic nutrient conditions and with a high water table (Moorschutzverein Pürgschachen, 2005).

2.2.5. Vegetation responses to drainage and succession pathways

Drainage-driven vegetation change in raised bogs is fundamentally a hydrology-mediated process. *Sphagnum* mats create and maintain the ombrotrophic, waterlogged conditions that favor further *Sphagnum* growth, so any persistent lowering of the near-surface water table breaks that positive feedback and opens the system to alternative vegetation states. This process can be described as a water-mediated vegetation switch. This conceptual frame explains why relatively small and/or persistent hydrological changes can produce large, self-reinforcing shifts in plant communities on bogs. (Frankl & Schmeidl, 2000; Rydin & Jeglum, 2013)

In many regions, drainage of raised bogs has been closely linked to forestry use, either through the construction of drainage ditches to improve tree growth or through the establishment of forest stands on formerly open bog surfaces. Studies from boreal and temperate forested peatlands show that vegetation responses to drainage in forestry-affected systems follow the same hydrologically driven pathways as described for open raised bogs. Typical responses include a decline of peat-forming *Sphagnum* species, an expansion of dwarf shrubs and graminoids, and a progressive increase in tree cover, ultimately leading to forest-dominated mire communities (Talbot et al., 2010; Maanavilja et al., 2014; Haapalehto et al., 2017). Although these studies were largely conducted in drained mire forests or spruce swamp forests, the reported vegetation changes are directly transferable to raised bog margins and forest-influenced raised bog systems, because the underlying driver is the persistent lowering of the water table.

While overall drainage induced degradation strongly effects plant structure and community composition, the pronounced effects depend on the severity of physical disturbance and water table drawdown (Haapalehto et al., 2017). The initial response to sustained drying is a decline of peat-forming *Sphagnum* species and an expansion of ericaceous dwarf shrubs and graminoids. Even slight lowering of the water table reduces *Sphagnum* growth and allows species such as *Calluna vulgaris* and *Eriophorum vaginatum* to spread across formerly peat-forming surfaces. (Eigner, 2003; Talbot et al.,

2010) Continued aeration of the upper peat and increased mineralization promote the development of *Molinia caerulea*, which often becomes dominant in intermediate degradation stages. As conditions become more favorable for plants requiring oxygenated rooting zones, trees begin to establish, most consistently *Betula pubescens*, but also *Pinus sylvestris*. and locally *Picea abies.* (Steiner, 2005) The progression of these species leads to the formation of full developed forest stages, which can eventually evolve into oak-birch forests. In these forests, *Molinia caerulea* typically dominates the herb layer, though in conditions of extreme dryness, *Deschampsia flexuosa* may prevail. These shifts mark the typical successional trajectory from open *Sphagnum* bog to heath, grass-dominated, and eventually woodland stages. (Eigner, 2003; Talbot et al., 2010)

Several species therefore function as reliable indicators of disturbance. An increasing or sudden presence of *Betula pubescens* or *Molinia caerulea* on bog surfaces strongly indicates persistent water-table lowering. Early dominance of *Calluna vulgaris* reflects the transition to a heath stage. Advancing establishment of *Pinus sylvestris,* or *Picea abies* signals late-stage succession toward bog woodland. (Eigner, 2003; Steiner, 2005) Because bryophytes respond tightly to microhydrological conditions, shifts from hydrophilic *Sphagnum* species to forest mosses also serve as sensitive indicators of drying and successional change. (Rydin & Jeglum, 2013; Dierßen & Dierßen, 2001).

Not all drained bogs follow the same pathway. Depending on peat structure, drainage intensity, landscape context, and the degree of nutrient enrichment through mineralization, degraded bogs may develop *Molinia* grasslands, birch-dominated woodland, pine woodland, or mixed dry heath communities. Some stages, such as the dominant stands of *Calluna vulgaris*, *Eriophorum vaginatum* or *Empetrum nigrum* can also occur in small areas in natural raised bogs and can hold conservation interest despite representing a loss of active peat formation ability. (Eigner, 2003)

In contrast, bogs that retain sufficient peat structure and hydrological integrity may undergo regenerative succession. Degraded but hydrologically restorable raised bogs, which correspond to FFH type 7120, can recover near-surface water tables and re-establish peat-forming vegetation if drainage impacts are reversed, potentially returning toward active raised bog within several decades. Successful recovery depends primarily on restoring acrotelm functioning and allowing recolonization by peat-forming *Sphagnum* species. (Eigner, 2003; Parish et al., 2008)

2.3. Ecological Indicator Values

2.3.1. Concept and application

Ecological indicator values provide numerical expressions of the realized ecological niche of plant species. The purpose of these values is to infer abiotic site conditions from species composition. This is rooted in the fundamental observation that plant species often show predictable relationships to key environmental gradients, such as soil moisture, pH, nutrients, and light. (Diekmann, 2003; Rydin & Jeglum, 2013) Plants integrate environmental conditions over time, meaning they often reflect the average state of their habitat more reliably than single-point measurements (Diekmann, 2003; Schaffers & Sýkora, 2000). This is particularly valuable where direct measurements would require substantial time investment or where historical baselines are unavailable.

Indicator systems such as *Flora indicativa* (Landolt et al., 2010) are based on extensive field experience and expert knowledge rather than experimental quantification. Despite this subjectivity, the values often correspond well with the realized optima of species along environmental gradients (Diekmann, 2003; Landolt et al., 2010; Schaffers & Sýkora, 2000). In the Alpine region, the Landolt system is particularly suitable because it includes many species absent from central European systems and, crucially for peatland studies, provides indicator values for bryophytes.

To characterize site conditions, indicator values for all species in a studied site can be combined into weighted mean indicator values, calculated as the cover-weighted average of all present species' indicator values (Diekmann, 2003). These weighted means summarize the ecological signal of the entire community and are widely used to infer moisture, pH, nutrient status, or light climate from vegetation composition. Because bryophytes lack roots and grow in direct contact with their substrates, their indicator values often respond particularly sensitively to hydrological gradients (Rydin & Jeglum, 2013; Landolt et al., 2010).

2.3.2. Relevance for peatlands

Peatland vegetation strongly reflects hydrological regime and trophic status, making indicator values especially useful for distinguishing ombrotrophic and minerotrophic conditions. The presence or absence of species with narrow ecological amplitudes, particularly the specialized bog species, allows reliable inferences about water level, pH, and nutrient status even when field visits occur during atypical hydrological phases (Rydin & Jeglum, 2013).

In drained or otherwise altered peatlands, indicator values help quantify the ecological shift away from typical bog conditions. Lower water tables, increased peat aeration and subsequent nutrient release alter species composition in predictable ways, which can be captured by weighted mean values for moisture, reaction, and nutrients (Diekmann, 2003; Ivanova & Zolotova, 2023; Rydin & Jeglum, 2013).

Because this study covers open bogs, bog woodlands and degraded peatland sections, indicator values offer a standardized, quantitative tool for comparing the degree of hydrological and trophic alteration across the landscape. Weighted mean indicator values thus provide an important complement to phytosociological classification by summarizing abiotic site tendencies directly from vegetation composition. (Ivanova & Zolotova, 2023)

2.3.3. Limitations

Despite their value, indicator systems have well-recognized constraints. Indicator values represent expert judgement rather than experimentally determined limits, and species may vary in their realized ecological responses across regions or vegetation types (Diekmann, 2003; Landolt et al., 2010; Schaffers & Sýkora, 2000). Weighted means can be misleading when plots contain strong microtopographic heterogeneity, common in peatlands with hummocks and hollows, because they may not reflect the conditions of any given microsite (Diekmann, 2003).

Vegetation may also lag behind environmental change, particularly in forested peatlands where long-lived species persist after hydrological alteration (Diekmann, 2003). Additionally, competition, dispersal limitations, and the absence of species with narrow ecological amplitudes can reduce the reliability of indicator-based assessments (Rydin & Jeglum, 2013).

Indicator values therefore provide integrative approximations rather than precise measurements and are best used in combination with direct environmental data where possible (Diekmann, 2003; Landolt et al., 2010). Within these limits, however, they remain a powerful tool for interpreting environmental gradients and hydrological alteration in peatlands.

3. Study site and regional setting

The study area comprises a drained and spruce-afforested section of approximately 10,000 m^2 situated on the former surface of an upland raised bog, as well as the directly adjacent, still-intact portion of the raised bog known as Krumauer Moor. This alpine-valley raised bog is located east of the town of Liezen in the Styrian Ennstal valley, at the margin of the Gesäuse National Park in the Austrian Alps. Administratively, the site lies within the municipality of Admont, between the settlements of Gesäuseeingang in the east and Krumau in the west, the latter giving the bog its name (Fig. 3.1). The exact coordinates of the study location are 47° 35' 1" N, 14° 30' 7" E (WGS 84).

Location of the study area Krumauer Moor in the eastern Styrian Ennstal valley

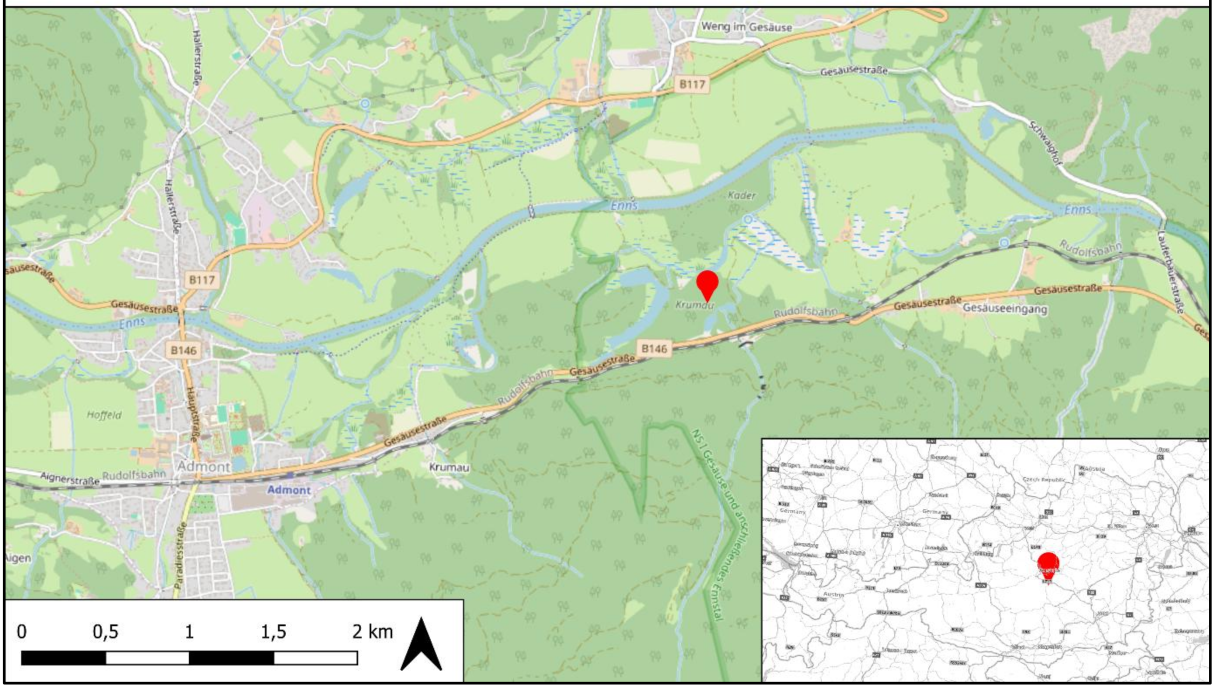

Figure 3.1: Location of the Krumauer Moor study area in the eastern Styrian Ennstal valley, as well as in the overall Austrian overview (Own illustration; Data source: OpenStreetMap contributors, 2025)

The site is positioned on the valley floor of the glacially shaped inner-alpine Ennstal, only about 500 m from the River Enns, at an elevation of approximately 626 m a.s.l., which is roughly 10 m above the current river level. It occupies the southern margin of the valley, separated from the northern slopes of the Reichensteiner massif only by the federal road B146 and a railway line. Several small mountain streams draining the adjacent slopes, such as the Schmiedelbach, flow through a series of ponds and backwaters surrounding the raised bog area (Fig. 3.1) before entering the eastward-flowing Enns.

In the satellite image (Fig. 3.2), the central raised bog appears as an open, sparsely wooded area embedded within a matrix of coniferous forests. Although the Ennstal region is generally dominated by agriculturally managed grasslands, the immediate surroundings of the bog are largely forested. The spruce-dominated stand in the northeastern part of the orthophoto, located between the forest road and the open bog, represents the drained and afforested section that forms the main focus of this study.

Figure 3.2: Orthophoto of the Krumauer Moor and surrounding area (Own illustration; Data basis and map program: Google LLC., 2025)

In the following subsections, the development, geomorphological formation, and present-day ecological conditions of the Krumauer Moor are described as the basis for the subsequent analyses.

3.1. Formation of the Enns Valley peatlands

The formation of the Krumauer Moor, as well as that of the other peatlands that line along the River Enns, began with the retreat of the Enns Glacier at the end of the last glaciation, approximately 10,000 years ago. This glacier, which reached its maximum extent around 20,000 years before present, followed a west-east oriented tectonic lineament formed during Alpine orogenesis and thereby carved the characteristic glacial trough of the Enns Valley.

With the progressive melting of the glacier, the valley floor was filled with glaciofluvial gravels and sands. Rockfalls and mass movements at the narrow gorge of the Gesäuse entrance repeatedly dammed the valley, leading to the formation of extensive proglacial lakes. The largest of these lakes are assumed to have extended westwards as far as the present-day municipality of Irdning. Over time, alluvial fans originating from tributary valleys subdivided these lakes into smaller water bodies, while the deposition of fine-grained sediments created water-retaining layers at the valley bottom.

As a result of ongoing territorialization processes, these smaller lakes gradually infilled with vegetation. In addition to swamp and floodplain forests, minerotrophic fens developed within the valley floor. In the context of the region's consistently humid climatic conditions, which permitted uninterrupted peat accumulation and progressive disconnection from groundwater influence, a few of these fens underwent a transition that culminated in the formation of ombrotrophic raised bogs. This sequence of postglacial landscape development ultimately led to the formation of the peatland complexes characteristic of the Enns Valley, including the Krumauer Moor (Jungmeier & Werner, 2004; Land Steiermark, n.d. b; Wintereder, 2017).

3.2. Historical land use

Although permanent settlement of the Enns Valley can be traced back at least to the Bronze Age, significant human impacts on raised bogs such as the Krumauer Moor did not occur until the 18th century. Prior to that time, settlement and land use were largely confined to alluvial fans and other slightly elevated areas above the valley floor. Due to the high precipitation regime of the region, the River Enns regularly flooded large parts of the valley bottom, rendering extensive use of peatlands and adjacent wet meadows impractical (Jungmeier & Werner, 2004; Tremel, 1960).

A major turning point for both the development of the valley landscape and the hydrological regime of the peatlands was the regulation of the River Enns, which actively began around 1860. River meanders were cut off, the channel was straightened, and tributary streams were engineered, resulting in a lowering of the water level by up to 1.5 m. These measures aimed to protect surrounding areas from flooding and to enable agricultural use of the valley floor (Tremel, 1960). From 1908 onwards, the deepening of the river channel facilitated large-scale drainage of the valley bottom. The lowering of the riverbed initiated a regional lowering of the groundwater table, indirectly affecting adjacent peatlands and fen systems. These interventions also influenced the Krumauer Moor. As early as 1910, it was reported that the bog complex lay 3-6 m above the water level of the regulated Enns, indicating a substantial alteration of its hydrological balance (Zailer, 1910).

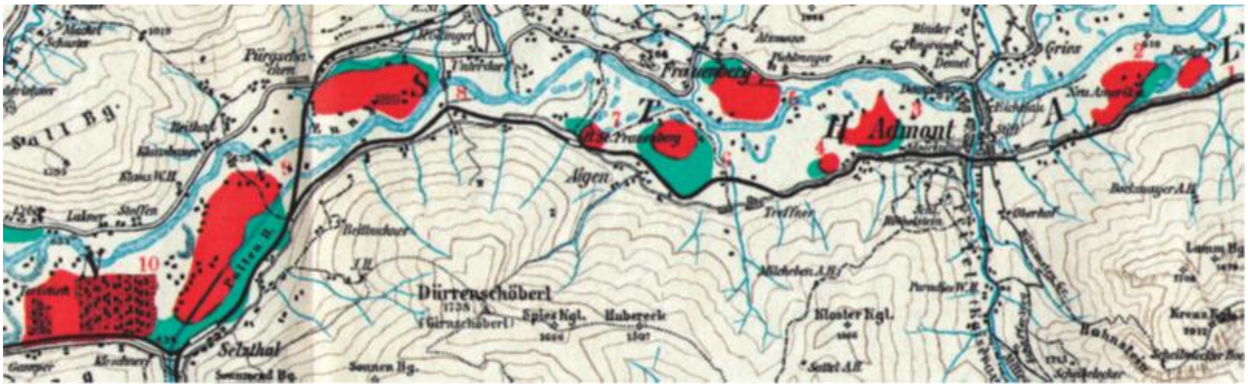

Figure 3.3: Excerpt from the map "Die Moore des Enns- und Paltentales", included in the 1909 Journal of Moorland Cultivation and Peat Utilization, shows the raised bogs where peat was harvested in red and the fens in green. At that time, they were named from right (Gesäuse entrance) to left (Liezen) as follows: 1 = Schmiedbacher-Moos (today Krumauer Moor), 2 = Neu-Amerika, 3 = Wolfsbacher-Moos (today Admonter Moorwirtschaft), 4 = Höllriegler-Moos, 5 = Pichlmayer-Moos, 6 = Dörfler-Moos (today Frauenberger Torfstich), 7 = Mödringer-Moos, 8 = Pürgschachen-Moos, 9 = Selzthaler-Moos, 10 = Gamper-Moos (Source: Hasitschka, 2013)

Even more severe impacts on the raised bogs of the Enns Valley, which were long regarded as economically unproductive land, resulted from peat extraction. From the 18th century onwards, peat was harvested on a large scale, primarily to supply fuel for the regional iron industry (see Fig. 3.3). The Krumauer Moor, which is owned by Admont Abbey, was also subject to early peat cutting. It is likely that this activity contributed to the formation of the Narrenteich and Scheibelteich, which are first documented in the Franzisco-Josephinian land survey (1869-1887) (see Fig. 3.4). Continuous demand for fuel culminated in the establishment of the peat extraction facility "Neu-Amerika" around 1870. By 1912, large parts of the former raised bog had been almost completely cut over, and peat extraction ceased shortly thereafter, coinciding with the increasing use of hard coal as an alternative energy source (Hasitschka, 2013).

Figure 3.4: Depiction of the Krumauer Moor in the Franzisco-Josephinian land survey (Source: Arcanum, n.d.)

Today, only a remnant of the former raised bog remains, which is also known as Schmiedbacher Moos, located east of the Scheibelteich. However, degradation processes did not end with the cessation of peat extraction. After the Second World War, renewed efforts were made to render these areas productive. As a result, strip drainage systems were installed and large parts of the former bog surface were afforested with spruce monocultures (*Picea abies*), further intensifying hydrological disturbance (Hasitschka, 2013).

These measures affected not only the previously cut-over sections of the Krumauer Moor, but also an area of approximately one ha at the eastern margin of the remaining raised bog. This drained and afforested site constitutes the focal area of the present study and is currently the target of ongoing revitalization efforts.

3.3. Development of nature conservation

Targeted nature conservation efforts for peatlands in the middle Enns Valley began in the 1990s in response to increasing drainage, afforestation, and agricultural intensification. Within the framework of the EU-funded LIFE project "Conservation of wetlands in the Enns Valley" (1995-1998), a network of wetlands of high conservation value was identified, including the Krumauer Moor. These sites were hydrologically assessed and subsequently secured for long-term protection through leasing, land exchange, and land acquisition measures (Bundesministerium für Land- und Forstwirtschaft, Regionen und Wasserwirtschaft, 2022).

The primary objective of the project was the preservation of ecologically valuable transition mires, raised bogs, and fens, as well as adjacent wet meadows and riparian forests. In parallel, existing drainage structures were partially removed or rendered ineffective, and conservation-oriented land-use practices were introduced, such as extensive mowing regimes. Through these measures, the LIFE project laid the foundation for the later integration of the mire and wetland complexes into the Natura 2000 network.

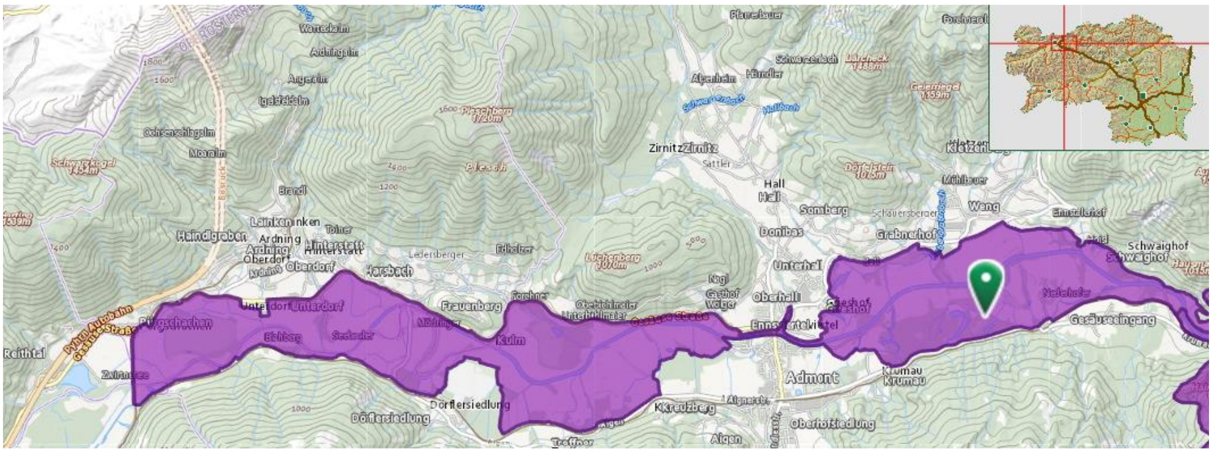

Figure 3.5: Location of the Krumauer Moor (green marker) in the Natura 2000 site "Pürgschachen-Moos and areas near the Enns between Selzthal and the Gesäuse entrance" in the eastern Enns Valley (purple) (Source: GIS-Steiermark, n.d. a)

The project laid the foundation for the subsequent inclusion of the peat- and wetlands in the Natura 2000 network. In 2003 and 2006, respectively, the area "Pürgschachen-Moos und ennsnahe Bereiche zwischen Selzthal und dem Gesäuseeingang" (AT2205000) (Fig. 3.5) was designated, which also includes the Krumauer Moor. (European Environment Agency, n.d.; Land Steiermark, n.d. c)

3.4. Abiotic site conditions

3.4.1. Climate of the study area

The study area at Krumauer Moor is located within the climatic region of the central Enns Valley, which is characterized by a pronounced inner-alpine, cool-temperate climate (Land Steiermark, n.d. a). Owing to its valley position at approximately 650 m a.s.l. and the shielding effect of the mountain ranges to the north, the area experiences long, cold winters with frequent temperature inversions and persistent fog conditions.

Based on long-term records of the Histalp station Admont (ADM) from 1994 to 2024 (GeoSphere Austria, n.d.), the mean annual air temperature is approximately 7.7 °C. The coldest month is January, with a mean temperature of −3.2 °C, while summer temperatures are moderate, with mean monthly values exceeding 17 °C in July and August (Fig. 3.6).

Precipitation in the Enns Valley is comparatively high due to frequent northerly airflow situations associated with orographic uplift. Mean annual precipitation generally increases from west to east and reaches its maximum in the Gesäuse mountain range east of the study area (Jungmeier & Werner, 2004). At the Admont station, close to the Krumauer Moor, mean annual precipitation amounts to approximately 1,238 mm. The highest monthly precipitation totals occur in mid-summer, with average values of about

165 mm in July and 152 mm in August, whereas spring months tend to be comparatively drier (Fig. 3.6).

The combination of cold winters, high summer rainfall, and frequent temperature inversions results in characteristic local microclimatic conditions within the peatland area. In particular, the region is marked by a high number of fog days during the winter half-year, with up to 120 fog days annually in parts of the valley. This pattern is related to reduced solar radiation in the valley floor compared to surrounding slopes and elevated areas, as well as to the high proportion of wetlands and oxbow waters within the landscape (Jungmeier & Werner, 2004; Land Steiermark, n.d. a).

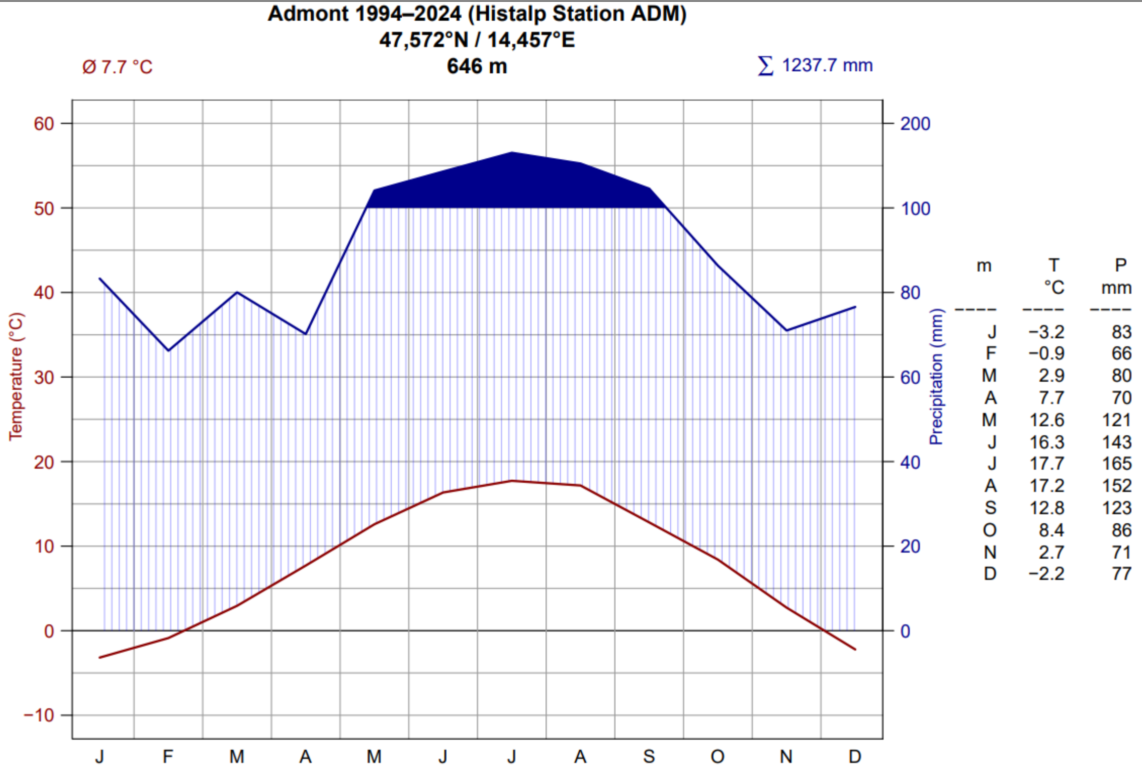

Figure 3.6: Climate chart for Admont in Styria, Austria (Own illustration; Data source: GeoSphere Austria, n.d.)

For contextualization, it should be noted that climatic conditions in the study area have changed measurably compared to the reference period 1961-1990, described in Jungmeier and Werner (2004). Mean annual air temperature has increased by approximately 0.9 °C relative to the former average of 6.8 °C. A similar shift is evident for both the warmest month (July) and the coldest month (January), for which mean temperatures have increased by roughly 1.5 °C. In contrast, mean annual precipitation shows only minor change, with current values exceeding those reported for 1961-1990 (1,227 mm) by approximately 10 mm.

3.4.2. Geology and geomorphology

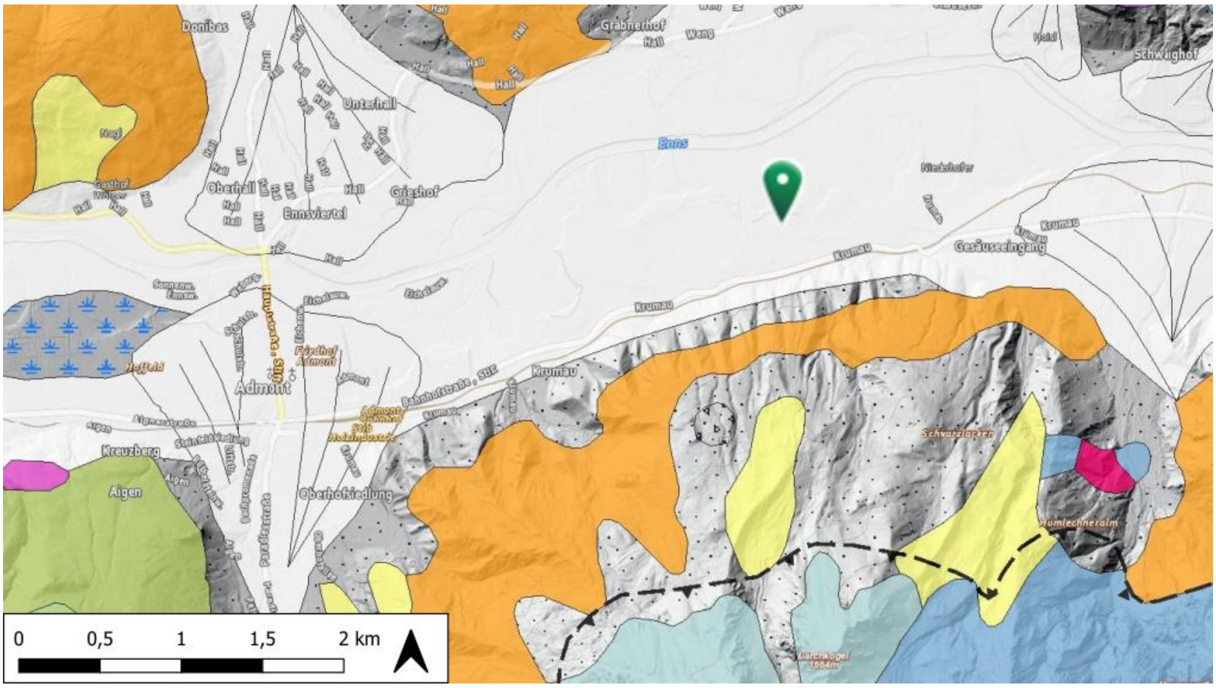

Figure 3.7: Geological situation around the Krumauer Moor (green marker). The different colored areas represent the geological formations: white - fluvial sediments from the Holocene (partly schematically marked as debris cones); colorless, dotted - slope debris and scree slopes, also of Holocene origin; yellow - Pleistocene moraine sediments; orange - quartzite, slate, limestone of the Werfen formation; dark blue - Wetterstein limestone, Wetterstein and Ramsau dolomite, light blue - Dachstein limestone; green - phyllites, spilite, diabase, green schist of the Grauwacke zone; pink - Blasseneck porphyroid of the Grauwacke zone (Source: GIS-Steiermark, n.d. b; modified)

From a geological perspective, the Enns Valley represents a major boundary between two contrasting geological units: the sedimentary formations of the Northern Calcareous Alps to the north and the metamorphic rocks of the Grauwacke zone to the south (orange and blue vs. green and pink areas in Fig. 3.7). The Grauwacke zone, which originated primarily during the Paleozoic, consists mainly of porphyroids, phyllites and schists containing quartz and hornblende. These lithologies are associated with comparatively gentle relief forms and rounded ridges and are also responsible for the regional occurrence of iron- and copper-bearing deposits. In contrast, the Northern Calcareous Alps are characterized by noticeably steeper and more rugged topography. They are composed predominantly of red sandstone, Werfen formation strata, dolomites and various other limestone units, all of which were deposited during the Mesozoic (Jungmeier & Werner, 2004).

This geological boundary between crystalline rocks and calcareous alpine units extends along the entire upper and middle Enns Valley, from the Salzburg state border eastwards to the municipality of Admont. In this area, the boundary follows a major fault zone and shifts approximately four kilometers southward, which is visible in Fig. 3.7 as the transition from green to orange geological units. As a result, the River Enns, constrained between the Haller Mauern massif to the north and the Reichenstein Mountains to the south, is forced to pass through the narrow gorge of the Gesäuse, which is entirely developed within calcareous alpine formations.

The study area itself is located on the valley floor along the northern slopes of the Reichenstein Mountains. Accordingly, the geological units occurring upslope of the Krumauer Moor include Quartzite, slate, and limestone from the Werfen layers, Dachstein and Wetterstein dolomites and limestones, as well as Holocene moraine deposits and slope debris (see Fig. 3.7; GIS-Steiermark, n.d. b).

Geomorphologically, as already mentioned, the Krumauer Moor is situated within a glacially shaped basin of the middle Enns Valley, whose development was strongly influenced by late- and postglacial processes. The valley fill consists of an approximately 200 m thick sequence of Quaternary unconsolidated sediments, dominated by gravels, sands and fine sediments. These deposits were created by fluvial processes associated with the River Enns and its former channel systems (Stelzhammer, 2008). In addition, alluvial fans formed by tributary streams from adjacent side valleys occur locally, such as the fan on which the settlement of Admont is located (see Fig. 3.7). As outlined above, this flat valley morphology with extensive terrace surfaces promoted the formation of poorly drained areas, thereby creating favorable conditions for the development of peatlands during the Holocene.

3.5. Current site conditions

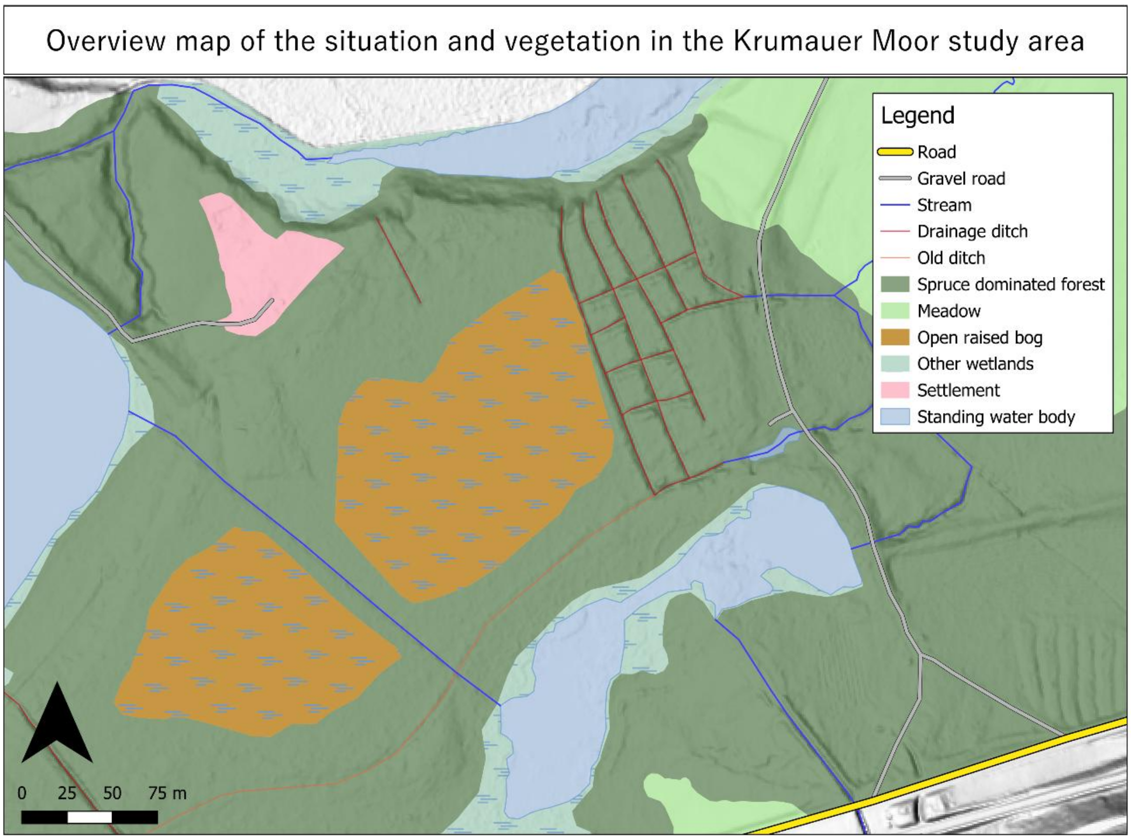

Figure 3.8: Overview map of the raised bog Krumauer Moor and its surroundings (Own illustration; Data source DGM: GIS-Steiermark, 2018)

The present-day remnant of the Krumauer Moor (depicted in Fig. 3.8) is located between the Narrenteich in the southeast, the Scheiblteich in the west, and an oxbow of the River

Enns to the north. This comparatively undisturbed raised bog area is surrounded by spruce-dominated bog woodland and spruce plantations, within which remnants of drainage ditches are still present, that are partially or fully infilled. As illustrated in Fig. 3.8, the open bog surface is intersected by a ca. 1.3 m deep channel that drains the Narrenteich. This channel most likely represents a small stream that may have developed along a water conveyance structure. Due to its gradient towards the Scheiblteich, progressive incision into the peat body can be observed locally.
According to the “Fachbericht Moore” for the Natura 2000 site “Pürgschachen-Moos und ennsnahe Bereiche zwischen Selzthal und dem Gesäuseeingang” (Moorschutzverein Pürgschachen, 2005), the raised bog area of the Krumauer Moor forms a mosaic of the habitat types Active raised bogs (7110), Degraded raised bogs still capable of natural regeneration (7120), and Bog woodland (91D0), with the first type occurring only in very small patches.

The western part of the open raised bog is largely dominated by *Pinus mugo*, the moss layer in this area is mainly composed of *Sphagnum angustifolium*. The larger, eastern part of the open bog, which represents the main intact reference area, contains several disturbance-associated species such as *Pinus mugo*, *Vaccinium myrtillus*, *Calluna vulgaris*, and *Molinia caerulea*. Nevertheless, it still exhibits a species composition typical of raised bog ecosystems. The moss layer is dominated by *Sphagnum magellanicum* and *Sphagnum angustifolium*, while characteristic species of the herb layer include *Vaccinium oxycoccos*, *Eriophorum vaginatum*, and *Andromeda polifolia*.
At the margins of the open raised bog, bog woodland occurs, with transitions ranging from gradual to relatively abrupt. The delimitation of these forest communities is challenging, as spruce-rich stands on peat are widespread throughout the surrounding area. For this reason, only spruce-dominated forest stands were distinguished in the overview map (Fig. 3.8). In the context of this study, bog woodland is defined operationally as forest stands within approximately 50 m of the open bog that show no clear signs of active drainage or intensive forestry use. These stands are dominated by *Picea abies*, accompanied by *Betula pubescens*, *Betula pendula*, and *Pinus sylvestris*. The shrub layer is mainly formed by *Frangula alnus*, while the herb layer is dominated by *Vaccinium myrtillus*. In addition, these sites are characterized by the presence of various forest moss species such as *Pleurozium schreberi* and *Hylocomnium splendens*, as well as locally occurring *Sphagnum* species.
Immediately east of the open raised bog lies the target area of ongoing revitalization efforts, which constitutes the main study area of this thesis. This approximately one ha site belongs to the part of the Krumauer Moor that was not completely affected by historical peat extraction, but it has been extensively drained by a grid-like system of drainage ditches (Fig. 3.8). In comparison with conventional drainage methods, the spacing between these ditches is particularly close, often ranging from 15 to 20 meters. The ditches were found to be approximately 1 to 1.5 meters deep, with the majority of them containing standing water and exhibiting substantial drainage activity towards the

edges. The material excavated during the construction of the ditches was piled up along them to form mounts that now measure approximately 1 meter in height. These drainage measures carried out around 60 years ago led to pronounced hydrological alteration, enabling the establishment of a *Picea abies* plantation and initiating peat mineralization processes. This is particularly evident on the peat mounts along the drainage ditches but can to some extent be observed on the flat former surface areas between the trenches.
Despite the strongly altered water regime, several moisture-indicating species persist in the understory of the spruce-dominated forest, including *Molinia caerulea* and various *Sphagnum* species. Within the drainage ditches themselves, which are largely characterized by permanently high groundwater levels, colonization by *Sphagnum angustifolium* can be observed, promoting ongoing natural infilling and local paludification.

4. Methodology

This chapter presents the methods used in the study to answer the research question. The following sections discuss the three central methods in detail, namely vegetation surveys, data analysis, and the writing process.

4.1. Field work

The aim of the field survey was to document vegetation changes and shifts in species composition caused by long-term, continuous drainage in a valley raised bog of the middle Enns Valley. Because drainage effects can only be interpreted in relation to a suitable reference state, the drained area was investigated in direct comparison with spatially adjacent reference sites. These reference sites were selected to be comparable in their general site conditions and landscape context but clearly differing in their disturbance history. The study therefore follows a comparative space-for-time approach, which is commonly applied as an indirect method in succession research. Although such indirect approaches do not allow explicit reconstruction of temporal development, as spatial differences cannot be interpreted as true temporal sequences, they represent a widely used and often the only feasible method for studying long-term vegetation dynamics (Dierschke, 1994).

The methodological framework followed the recommendations for vegetation surveys provided by Dierschke (1994). Accordingly, an initial assessment of the study area was conducted in order to define suitable sampling locations, determine the number and timing of surveys, and establish a standardized field procedure. Three vegetation types were investigated: the bog area drained for spruce plantation after the Second World War (*drained bog site*), the adjusting remaining open raised bog used as a reference for largely undisturbed conditions (*open bog site*), and the neighboring bog-forest transition zone (*bog forest site*). In addition to vascular plants, bryophytes were recorded, but only ground-dwelling species were considered, while lichens, epiphytic mosses and algae were excluded.

The open bog was selected to represent vegetation conditions that most closely resemble the original raised bog state prior to drainage, whereas the bog forest was included as a reference for naturally forest-influenced bog vegetation occurring at the margins of the open bog. Together, these two reference sites were intended to bracket the range of vegetation states against which the drained area could be interpreted.

Because not all species of a plant community are visible or dominant at a single point in time, vegetation surveys were conducted at two dates within the vegetation period (March-October), once in spring (May) and once in late summer (August). This was done to capture a more complete species inventory and to account for phenological differences among species.

Following the first field assessment, the final selection and delineation of vegetation plots was carried out. According to Dierschke (1994), plot selection can be based on systematic, random or subjective approaches. In the drained area, a stratified sampling design was applied, because different microtopographic features (drainage ditches, former bog surfaces and peat mounts) occur only at very small spatial scales. These features were first identified and checked for vegetation homogeneity, and plot centers were then placed in an unbiased manner within each feature type. In contrast, in the open bog and bog forest sites, where vegetation cover was largely homogeneous, random plot selection within carefully delineated areas was applied.

4.1.1. Selection of study sites

A first field assessment of the broader study area was conducted on 04 April 2025. During this survey, a general vegetation mapping of the entire study area was carried out, resulting in a vegetation map used for subsequent site selection (Fig. 3.8, Chapter 3.5.). Digitization and cartographic processing were performed using QGIS Desktop (version 3.44.0).

The mapping was supported by field sketches and photographs, current satellite imagery from Google Earth (Google LLC., 2025), orthophotos provided by Geoland (2025) and a digital elevation model obtained from GIS-Steiermark (2018).

Vegetation units were delineated based on the dominant vegetation structure. As shown in Figure 3.8, the following main vegetation types were distinguished: open raised bog, spruce-dominated forest, meadow and other wetlands. In addition, areas classified as settlement and standing water bodies were mapped.

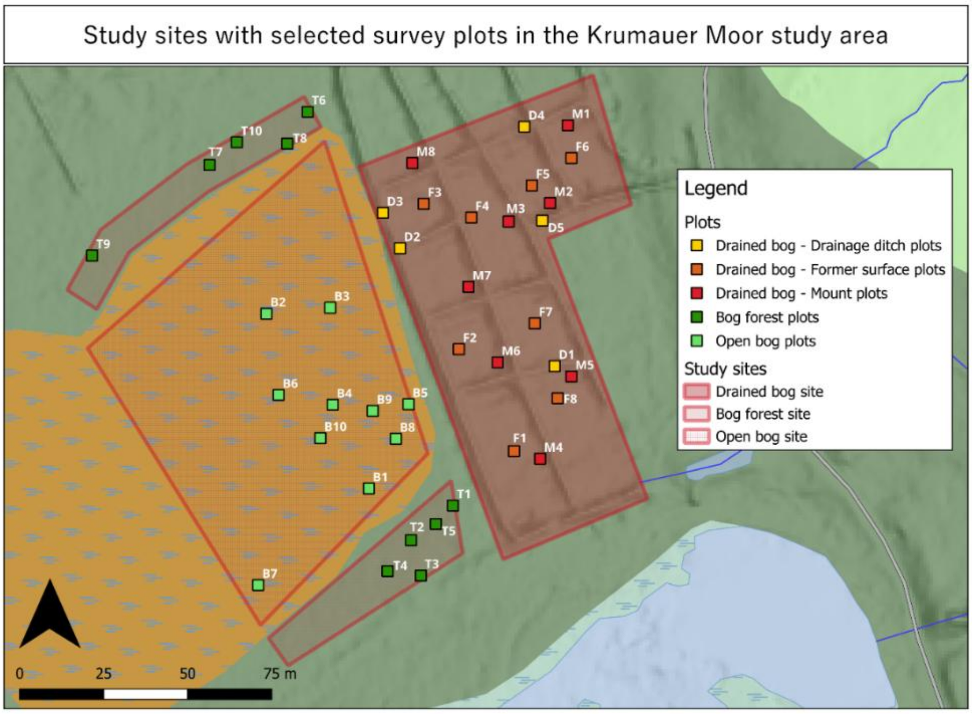

Figure 4.1: Map of the study area showing the study sites and the associated plots for vegetation surveys (Own illustration; Data source DGM: GIS-Steiermark, 2018)

During the first field assessment, drainage ditches were mapped and differentiated into apparently active and older, apparently inactive ditches. Small streams and access tracks were also recorded and included in the overview map (Fig. 3.8).

Based on this mapping, the three study sites were defined as shown in Fig. 4.1.

The open bog site comprises a largely open raised bog area with very low tree cover and only scattered individual trees. The transition to adjacent forest is abrupt and characterized by a denser and taller herb and shrub layer. Areas dominated by *Pinus mugo* were included within the open bog site. The eastern boundary towards the drained area is marked by a strip of shrubs and trees along the westernmost drainage ditch.

The bog forest site consists of forest strips located north and south of the open bog area. These strips are approximately 25-50 m wide and directly border the open bog. The northern boundary is defined by a terrain edge, while the southern boundary is formed by the transition towards riparian vegetation surrounding an adjacent pond. A well-developed shrub layer is present at many locations. With few exceptions, which were considered during plot selection, no active drainage ditches were observed within the bog forest site.

The drained bog site is located east of the open bog and is intersected by a dense network of active drainage ditches arranged in a grid-like pattern. The approximately 1 ha area is characterized by planted *Picea abies*. The understory vegetation is heterogeneous but generally forms a dense shrub layer. The northern boundary is defined by a terrain drop towards a former river arm, while the southern boundary is marked by ponds. The eastern boundary coincides with a gravel road.

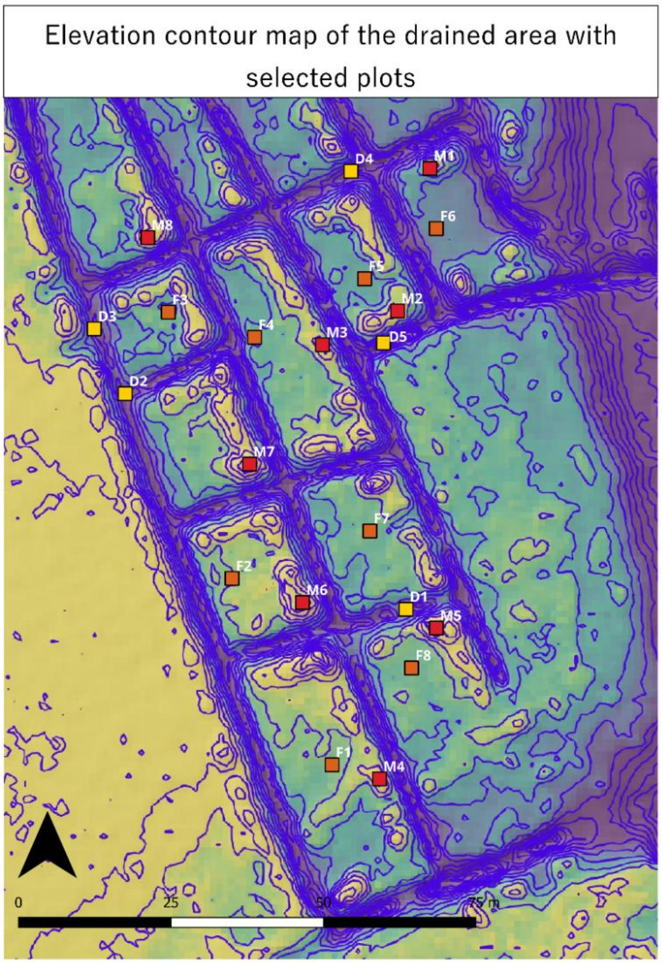

Figure 4.2: Drained bog site with marked plots (red - mounts; orange - former surfaces; yellow - drainage ditches) and elevation contour map showing the terrain features (Own illustration; Data source: Mag. Joachim Brocks)

An attempt to map the microtopographic features of the drained site by field scanning proved unsuccessful due to dense understory vegetation and difficult accessibility. Instead, a hillshade relief map was used to identify microtopographic structures, which are clearly visible in the digital elevation model (Fig. 4.2) and served as the basis for plot selection.

For the open bog and bog forest sites, rectangular sampling areas were defined within the sites (Fig. 4.1). One rectangular area was delineated within the open bog, and two within the bog forest (north and south of the open bog). All sampling areas were placed well within the boundaries of the respective vegetation units to minimize edge effects. The sites were selected in close spatial proximity to each other and to the drained site in order to ensure comparable regional and geomorphological conditions. At the open bog site, no stratification by microtopographic features was applied, as this site served primarily as a reference for overall vegetation composition and cover. Consequently, both hummock and lawn microforms were included within the randomly selected plots.
Within each rectangular area, ten plot centers were selected at random. For the bog forest site, five plots were allocated to the northern and five to the southern forest strip. Random coordinates were generated using an R script that selects random points within a polygon defined by known corner coordinates. The resulting coordinates represent the centers of the vegetation plots and are provided in Appendix C.
Within the drained bog site, three distinct microtopographic feature types were distinguished: drainage ditches (approximately 1 m deep), former bog surface (flat areas between ditches), and mounts created by peat excavated from the ditches and deposited alongside them (approximately 0.5 m above the former bog surface). Due to the small spatial extent and pronounced heterogeneity of these features, a stratified random sampling design was applied. Plot centers were selected separately for each feature type based on the relief map shown in Figure 4.2. In total, five plots were placed in drainage ditches, eight on mounts and eight on former bog surface areas. The number of plots per feature type was chosen to adequately represent the vegetation characteristics of the respective microhabitats.

4.1.2. Vegetation survey

Vegetation was recorded twice per plot, once in late spring (27-28 May 2025) and once in late summer (23-24 August 2025), in order to capture the full range of species occurring during the growing season.
A standardized vegetation recording sheet was used (Appendix B), following the recommendations of Dierschke (1994). Recorded information included plot identification (B = open bog; T = bog forest; M = mounts; F = former surface; D = drainage ditch), site remarks, estimated canopy cover, date and time of recording, and weather conditions.
For each species, a unique species ID was assigned when identification was uncertain and photographic documentation was required for later determination. Species cover was estimated using a modified Braun-Blanquet abundance-dominance scale with twelve cover classes (Table 4.1). The use of intermediate cover classes allows a finer representation of percentage cover and improves reproducibility of quantitative analyses (van der Maarel, 1979; Wikum & Shanholtzer, 1978).

Table 4.1: Abundance-dominance scale with twelve cover classes, based on Braun-Blanquet (Source: Dierschke, 1994; modified)

Scale	Description	Mean cover in %
5	Any number of individuals, coverage >75%	87.5
4(5)/5(4)		75
4	Any number of individuals, coverage 50 - 75%	62.5
3(4)/4(3)		50
3	Any number of individuals, coverage 25 - 50%	37.5
2(3)/3(2)		25
2	Large number of individuals with low coverage or coverage 5 - 25%	15
1(2)/2(1)		5
1	Abundant number of individuals with low coverage or sparse number of individuals with greater coverage	2.5
+(1)/1(+)		1.5
+	Sparse number of individuals with low coverage	0.5
r	Isolated individuals	0.1

During the first survey, the coordinates of all plot centers were located in the field using a handheld GPS device. Plot centers were marked with flags for relocation during the second survey and documented photographically (Fig. 4.3).

Each vegetation plot measured 1 x 1 m. The plot frame was constructed in the field using two folding rulers of two meters length, bent at right angles and arranged around the plot center (Fig. 4.3).

Figure 4.1: Survey situation at plot B10 (Own image)

All vascular plant and bryophyte species with at least part of their above-ground biomass located within the plot area were recorded. Species cover was estimated as percentage cover of the entire plot area using the modified Braun-Blanquet scale. Furthermore, the vegetation layer in which each species was found was recorded, distinguishing between moss, herb, shrub, and tree layers. In some cases, tree and shrub species were assigned to several layers due to the different heights of individual plants, with separate degrees of coverage being recorded.

Vascular plant species were identified primarily in the field using, the mobile application iNaturalist (iNaturalist, n.d.). Photographs were uploaded or taken directly in the application, and automated image recognition was used to generate candidate species

lists. All automated suggestions were critically evaluated and verified using morphological characters and distribution information. In addition, the “Exkursionsflora für Österreich, Liechtenstein und Südtirol” (Fischer et al., 2008) was used to support field identification.
Species lists were further cross-checked with the vegetation inventories compiled for the Natura 2000 site “Pürgschachen Moos und ennsnahe Bereiche zwischen Selzthal und dem Gesäuseeingang” (Moorschutzverein Pürgschachen, 2005).
In the main text, species names are presented without author citations. Full author citations for all recorded species are provided in Table 5.1.
The selection of species classified as typical raised bog species and as disturbance indicators was based on the indicator species lists for raised bog communities provided by Steiner (2005) and on characteristic species for Austrian FFH habitat types compiled by Ellmauer and Traxler (2001), supplemented by information from Eigner (2003).

Bryophytes were identified using a combination of field characters, photographic documentation and microscopic examination. For moss determination, identification keys and resources provided by the webservice of the British Bryological Society (2021) were consulted, complemented by standard field guides. Specimens were collected where necessary and examined under a light microscope.
Particular emphasis was placed on the identification of *Sphagnum* species. Determination followed a detailed assessment of macro- and micromorphological characters, including growth form, plant size, color of capitula and stems, branch differentiation, stem leaf morphology and branch leaf shape. Microscopic characters such as leaf structure, hyaline cell features and cell pore patterns were examined using hand sections and light microscopy. For each identified *Sphagnum* species, photographic documentation was compiled, including field photographs of growth forms and habitat conditions and microscopic images of diagnostic characters. The results, including the images, are presented in chapter 5.1.2. and in the Appendix A.
Species determination was carried out using established identification literature and keys (Daniels et al., 1985; Smith & Smith, 2004; Zechmeister, 1995). Special attention was given to taxa belonging to species aggregates (e.g. *Sphagnum recurvum* agg.) and to the distinction between peat-forming *Sphagnum* species and non-peat-forming forest mosses. Selected *Sphagnum* determinations were validated during a field excursion by Prof. Steiner, an expert for *Sphagnum* mosses in Austria.

4.1.3. Environmental data collection

Environmental site parameters were recorded in order to characterize the main abiotic gradients associated with drainage and to support the interpretation of vegetation patterns. For each vegetation plot, one peat sample was collected on 05 June 2025.
Sampling was conducted directly within the 1 x 1 m vegetation plots, while making sure to not disturb the vegetation. Subsamples of peat, comprising three to five individual replicates, were combined to generate a mixed sample for each plot. The material was

taken from the upper peat layer, targeting the biologically active 15 to 20 cm surface horizon of the bog. This surface layer is considered most relevant for most plant rooting conditions and short-term hydrological responses.

From each sample, gravimetric water content, degree of peat decomposition and soil reaction (pH) were determined.

Gravimetric water content was measured by drying the peat samples at 105 °C until constant weight and calculating the relative water content based on fresh and dry mass. This approach provides an estimate of the actual moisture conditions of the surface peat layer at the time of sampling.

The degree of peat decomposition was assessed in the field using the Von Post humification scale (Tab. 4.2), following the descriptions of Succow and Joosten (2001) and Caspers (2010). The classification was based on the visual and tactile properties of the peat, including color of the expressed water, fiber content and the degree of structural breakdown during manual squeezing. The Von Post scale was used as an established semi-quantitative indicator of peat aeration and long-term drainage effects.

Table 4.2: Von Post Scale for determination of degree of humification (Source: Caspers, 2010 [Translated])

Degree of humification	Description	Squeezing method
H1	Completely undecomposed peat	When squeezed in the fist, colorless, clear water runs between the fingers
H2	Almost completely undecomposed peat	When squeezed, almost clear, only slightly yellow-brown water comes out
H3	Very weakly decomposed peat	When squeezed, clearly turbid, brown water, but no peat substance between the fingers; residue not muddy
H4	Weakly decomposed peat	When squeezed, produces very muddy water, but no peat substance is released; residue is somewhat muddy
H5	Rather decomposed peat; plant structure still clearly visible	When squeezed, some peat substance is released, but mainly cloudy, brown water; residue is very muddy
H6	Rather decomposed peat; plant structure indistinct	When squeezed, up to 1/3 of the peat substance is lost; residue is very muddy, but with a more pronounced plant structure than in unpressed peat
H7	Strongly decomposed peat	When squeezed, half of the peat substance is lost; plant structure still relatively recognizable
H8	Very strongly decomposed peat	When squeezed, 2/3 of the substance is lost between the fingers; plant structure very indistinct; residue mainly consists of resistant plant material, such as root fibers, wood, etc.
H9	Almost completely decomposed peat	Almost all of the peat mass slips out between the fingers when squeezed; hardly any plant structure is recognizable
H10	Completely decomposed peat	When squeezed, the entire mass slips through between the fingers; no plant structure is recognizable

Soil reaction (pH) was determined directly in the field from water extracted from the peat samples by manual squeezing. Measurements were carried out using a portable field pH meter. This procedure allows a rapid approximation of the chemical conditions in the near-surface peat layer and avoids potential alterations caused by storage or transport.

In addition to the soil parameters, vegetation-related structural variables were recorded for each plot during the vegetation survey. These included visually estimated canopy density above the plot, total tree cover derived from the summed cover values of all tree species, as well as total cover of Sphagnum species and of non-peat-forming forest mosses. These variables were later used to relate vegetation composition to both hydrological conditions and shading effects.

All environmental parameters were recorded once per plot and were assumed to represent the general site conditions of the respective microhabitats during the study period. The complete set of collected data is available for reference in Appendix E.

4.2. Data analysis

All vegetation records were digitized in Microsoft Excel and stored in separate datasets for the two sampling campaigns (May and August). The original field sheets headers including the plot metadata and the complete digitalized vegetation tables are provided in Appendix C and D.

All subsequent data processing and statistical analyses were conducted in R (RStudio version 2025.09.2, Build 418), mainly using the packages *vegan* and *tidyverse*. Parts of the R code used for data processing and statistical analyses were developed with the assistance of ChatGPT (OpenAI, 2025). The AI tool was used to support code formulation, debugging and optimization, while all analytical decisions, data interpretation and final methodological implementations were made by the author.

The analytical workflow consisted of three main steps. First the data preparation and evaluation of seasonal effects, then the community-based analyses including plant community assignment, and calculation and further the evaluation of cover-weighted Landolt indicator values and their relationships with measured environmental variables.

4.2.1. Data preparation and assessment of seasonal effects

Vegetation was surveyed twice (May and August) in order to account for possible seasonal differences in species occurrence and cover. Species cover data from both surveys were first transformed into a long data format and standardized across both sampling dates.

To assess whether seasonal effects influenced the vegetation data, species richness per plot was compared between the two sampling dates using a paired Wilcoxon signed-rank test In addition, potential differences in overall species composition between the two surveys were tested using a permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities implemented in the *adonis* function of the *vegan* package (Anderson, 2017; Oksanen et al., 2024).

As neither species richness nor community composition differed significantly between the two sampling campaigns, seasonal effects were considered negligible. Minor seasonal differences in the occurrence and cover of individual species were addressed descriptively in the Results chapter.

For all further analyses, species cover values were averaged across the two sampling dates for each plot and species. To avoid pseudo-replication and double counting in subsequent analyses, a single representative mean cover value per species and plot was used.

Furthermore, for all analyses based on total species cover per plot (e.g. dominance patterns and indicator value calculations), cover values of species recorded in more than one vegetation layer were first summed across layers prior to averaging across the two sampling dates.

4.2.2. Plant community assignment and synoptic comparison

Species composition was analyzed at the level of the three site types (open bog, bog forest and drained bog) and, within the drained bog, separately for the different drainage-related microtopographic features (mounts, former surfaces and drainage ditches).

For each species, frequency (constancy) and mean cover were calculated for every site type and feature group based on the pooled and averaged plot data. These values were used to compile synoptic tables describing species occurrence patterns and dominance structures for the different vegetation units.

Plant community affinities were assessed using a synoptic comparison of species composition, constancy patterns, dominance relationships and general vegetation structure. The assignment to syntaxonomic units followed the diagnostic species concept and the syntaxonomic framework described by Steiner (1992), considering vegetation classes, orders, alliances and associations where applicable.

In addition, the web-based tool „Pflanzengesellschaften suchen" (Ökologie-Seite, 2025) was used to support the identification of potential vegetation units. For this purpose, site-specific species lists were uploaded and compared with reference species lists stored in the database.

Both approaches were applied in a complementary manner and served to guide the syntaxonomic interpretation. No formal plot-based phytosociological classification was performed, as the investigated vegetation showed pronounced transitional characteristics and was strongly influenced by long-term disturbance and successional processes. The results of the community assignment therefore represent ecologically interpreted vegetation units rather than strictly defined associations.

4.2.3. Multivariate analysis of vegetation composition

For multivariate analyses, vegetation cover data from both sampling campaigns were first averaged per species and plot to obtain one representative cover value per plot and

species. Based on these values, a species-by-plot community matrix was constructed and used as input for all subsequent multivariate analyses.
Compositional differences among plots were quantified using Bray-Curtis dissimilarity, which is appropriate for quantitative vegetation data and insensitive to joint absences.
Non-metric multidimensional scaling (NMDS) was applied to visualize multivariate patterns in species composition and to represent similarities among plots in a reduced ordination space. Ordinations were calculated using the function *metaMDS* implemented in the *vegan* package. The quality of the ordination was assessed using the final stress value.
To test for differences in species composition among groups, permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities was performed using the function *adonis2* with 999 permutations.

To identify which measured site parameters were related to the observed compositional gradients, environmental variables were fitted onto the NMDS ordination using the function *envfit* (999 permutations). The fitted variables included topsoil water content, degree of peat decomposition (Von Post scale), soil pH and canopy density.
Only directly measured site parameters were included as explanatory variables. Variables derived from the vegetation data itself (tree cover, *Sphagnum* cover and forest moss cover) were excluded in order to avoid circularity between response and explanatory variables.
Ordination plots were produced to visualize the distribution of plots according to site types and drainage-related microtopographic features and the orientation and relative strength of significant environmental gradients.

4.2.4. Calculation and analysis of Landolt indicator values

Ecological indicator values according to Landolt et al. (2010) were used to derive vegetation-based estimates of site conditions. The Landolt system was selected because it is specifically calibrated for the Alpine region and includes indicator values for both vascular plants and bryophytes, which is essential for peatland studies.
Indicator values were compiled for all recorded species for the following variables: temperature (T), light (L), moisture (F), reaction (R), nutrients (N), and humus (H). The respective description of the indicator value scales for vascular plants and bryophytes according to Landolt et al. (2010) can be found in Appendix F.
These values were extracted for all vascular plant and bryophyte species recorded in the vegetation surveys. Species without assigned or indifferent Landolt indicator values were excluded from the indicator value analyses, following standard practice.
Because different indicator systems and ecological scales apply to vascular plants and bryophytes, indicator values were treated separately for the two taxonomic groups.

The use of indicator values from multiple species has been shown to provide more accurate and reliable indications compared to those derived from a single species

(Diekmann 2003). The determination of Landolt indicator values for a given plot or site is most accurately achieved by considering the full composition of present plant species. However, the utilization of simple averages of the values of all plant species is not a suitable approach, as these would not take into account the abundance of the respective plant species. Therefore, in the present study, the weighted mean values were calculated using the coverage degree estimated based on the Braun-Blanquet scale. Cover-weighted mean Landolt indicator values were computed according to

$$mZ = \frac{\sum(Z \times C)}{\sum C}$$

where *Z* is the indicator value of a species and *C* is its percentage cover.

To avoid double counting of species occurring in different vegetation layers, species cover values were first aggregated per plot by summing the cover values of all layers for each species. Subsequently, the aggregated species cover values were averaged across the two sampling dates (May and August). These season-independent mean cover values were used for the calculation of all indicator values.
Community-weighted Landolt indicator values were calculated for all selected indicator variables. These values were calculated separately for each vegetation plot and for each taxonomic group (vascular plants and bryophytes). The distribution of cover-weighted Landolt indicator values was analyzed descriptively among the three site types (open bog, bog forest and drained bog), and among the drainage-related microtopographic features within the drained bog (mounts, former surfaces and drainage ditches).
Differences among site types and feature groups were visualized using boxplots for each indicator variable and taxonomic group.

4.2.5. Relationships between indicator values and measured environmental variables

To evaluate whether vegetation-based indicator values reflect measured site conditions, correlations were calculated between cover-weighted Landolt indicator values and selected environmental variables measured in the field.
The following ecologically corresponding indicator-environment pairs were analyzed:

- moisture indicator (F) with gravimetric soil water content and degree of peat decomposition (Von Post scale),
- light indicator (L) with canopy density,
- nutrient indicator (N) with soil pH and degree of peat decomposition, and
- reaction indicator (R) with soil pH.

Correlation analyses were conducted separately for vascular plants and bryophytes to account for differences in indicator systems and ecological interpretation between the two taxonomic groups.

Non-parametric Spearman rank correlations were applied because several variables were not normally distributed and because both indicator values and some environmental variables represent ordinal or semi-quantitative scales.
To account for multiple testing, p-values were adjusted using the Holm correction. Correlation patterns were visualized using scatterplots with fitted trend lines.

4.3. Literature review and writing process

To ensure transparency and traceability of the literature work, the following section provides a brief overview of the search strategy and writing process applied in this thesis. A complete list of all cited sources is provided in the reference section.

The literature review was conducted using a structured keyword-based search approach in both German- and English-language sources. Searches were carried out using the University of Vienna library search service (u:search) as well as Google Scholar. Keywords included combinations of terms related to peatlands, raised bogs, drainage, succession, peat decomposition, vegetation change, restoration, ecological indicator values and alpine peatland systems.
In addition to systematic keyword searches, a snowball sampling strategy was applied by screening reference lists of relevant publications to identify further pertinent literature. Previously known key publications in peatland ecology were also incorporated where relevant.
To support targeted identification of peer-reviewed studies, the AI-powered academic search engine *Consensus* (Consensus, 2026) was used as a supplementary tool. This tool facilitated efficient screening of research questions and synthesis of scientific findings. All literature identified through AI-assisted search tools was critically evaluated and cross-checked using primary sources before inclusion in the thesis.
Despite extensive research efforts, no studies were identified that specifically address drainage-induced vegetation change caused by forestry drainage in alpine raised bog systems within the investigated region. More generally, comparable studies on long-term drainage effects in alpine raised bogs in Central Europe are scarce. Consequently, the discussion partially refers to studies from ecologically comparable peatland systems in other climatic regions, particularly boreal and temperate peatlands, while carefully considering differences in climate and site conditions.
All references were cited according to APA guidelines.

The writing process was supported by digital language tools. For translation and language refinement, the translation service DeepL and the AI-assisted writing tool DeepL Write (DeepL SE, 2026) were used. In addition, parts of the R code for data processing and statistical analyses were developed with the assistance of the AI-based language model ChatGPT (OpenAI, 2025), as described in Section 4.2. The use of AI tools was limited to technical and linguistic support. All conceptual decisions, scientific interpretations and final formulations remain the responsibility of the author.

5. Results

5.1. Floristic overview and species composition

A total of 39 plant species were recorded across all sampled plots, comprising 17 bryophytes and 22 vascular plant species. Bryophytes represented a substantial component of the recorded flora and included both peat-forming *Sphagnum* species and a range of non-peat-forming mosses. The vascular plant assemblage consisted of herbaceous and woody species characteristic of raised bogs, bog forests, and drained peatland conditions. A complete list of all recorded species, including taxonomic authorship, is provided in Table 5.1.

Table 5.1: List of all identified plant species in the study area; sorted by taxonomic group

Species list of the study area Krumauer Moor
Scientific name:
Bryophytes:
Aulacomnium palustre (Hedw.) Schwägr.
Bazzania trilobata (L.) Gray
Dicranella heteromalla (Hedw.) Schimp.
Dicranum scoparium Hedw.
Hylocomium splendens (Hedw.) Schimp.
Leucobryum glaucum (Hedw.) Ångstr.
Plagiochila asplenioides (L.) Dumort.
Plagiomnium ellipticum (Brid.) T.J.Kop.
Plagiomnium undulatum (Hedw.) T.Kop.
Plagiothecium undulatum (Hedw.) Bruch, Schimp. & W.Gümbel
Pleurozium schreberi (Brid.) Mitt.
Polytrichum formosum Hedw.
Rhytidiadelphus loreus (Hedw.) Warnst.
Sphagnum angustifolium (Warnst.) C.E.O.Jensen
Sphagnum capillifolium (Ehrh.) Hedw.
Sphagnum magellanicum Brid.
Syntrichia ruralis (Hedw.) F.Weber & D.Mohr
Vascular plants:
Acer pseudoplatanus L.
Andromeda polifolia L.
Betula pendula Roth
Betula pubescens Ehrh.
Calluna vulgaris (L.) Hull
Carex rostrata Stokes
Dryopteris dilatata (Hoffm.) A.Gray
Dryopteris expansa (C. Presl) Fraser-Jenk. & Jermy
Eriophorum vaginatum L.
Fagus sylvatica L.
Frangula alnus L.
Melampyrum pratense L.
Molinia caerulea (L.) Moench
Picea abies (L.) H.Karst.
Pinus mugo Turra
Pinus sylvestris L.
Quercus robur L.
Sorbus aucuparia L.
Vaccinium myrtillus L.
Vaccinium oxycoccos L.
Vaccinium uliginosum L.
Vaccinium vitis-idaea L.

The recorded flora comprised a heterogeneous assemblage of bryophytes and vascular plants, reflecting a range of hydrological and structural conditions within the study area. Bryophytes accounted for a substantial proportion of the species pool and included both peat-forming *Sphagnum* species and non-peat-forming mosses. Among bryophytes, *Sphagnum* species represented a distinct functional group characterized by their dominance in the moss layer of open and weakly forested sites, whereas non-peat-forming mosses were mainly associated with forest-influenced and drained conditions.

The vascular plant assemblage included both herbaceous and woody species. Herbaceous species were primarily composed of graminoids and dwarf shrubs typical of raised bogs and bog forests, while woody species included both shrubs and trees adapted to acidic, nutrient-poor peat substrates. Several vascular plant species occurred across multiple habitat types, whereas others were restricted to specific site conditions.

Overall, the floristic composition encompassed species typical of intact raised bogs as well as taxa associated with forest influence and drainage-related disturbance. This mixture of species groups provided the basis for the subsequent site- and feature-specific analyses presented in the following sections.

5.1.1. Bryophytes

Bryophytes constituted an important component of the recorded flora and comprised both peat-forming *Sphagnum* species and non-peat-forming mosses. In the following sections, *Sphagnum* species and forest mosses are summarized separately to reflect their functional and ecological differences.

5.1.1.1. Sphagnum species

A total of three *Sphagnum* species were identified within the study area, representing the sections *Cuspidata*, *Acutifolia*, and *Sphagnum*. All recorded species are peat-forming mosses and can be classified as typical taxa of raised bogs, constituting key structural components of the vegetation. Species identification was based on macro- and micromorphological characteristics using standard determination literature (e.g. Daniels et al., 1985; Smith & Smith, 2004; Zechmeister, 1995). Microscopic images of diagnostic features and the corresponding references from the identification literature can be found in Appendix A.

Sphagnum magellanicum (Fig. 5.1) was by far the most frequent and cover-dominant species and was recorded in all investigated site types. In the open bog, it occurred in all

Figure 5.1: Different situations and forms of Sphagnum magellanicum. Wine-red specimens in open bog (A), typical hummock (B), and almost completely green specimens in the forest of the drained site (C) (Own images)

plots and frequently reached high cover values, often forming extensive, continuous carpets or low hummocks (see Fig. 5.1 B). The species was also regularly present in the bog forest, although typically with lower cover. Within the drained bog, *S. magellanicum* occurred mainly on former bog surfaces and, more sporadically, on mounts; in addition, it was recorded in drier sections of drainage ditches, particularly in transitional zones adjacent to the open bog. As depicted in Figure 5.1, pronounced site-dependent differences in coloration were observed, plants in the open bog were predominantly deep wine-red, whereas individuals in shaded bog forest conditions were usually entirely green.

Ecologically, *S. magellanicum* is a characteristic species of oligotrophic raised bogs, strongly acidophilous, and typical of the class *Oxycocco-Sphagnetea*. The species exhibits a rather high tolerance to water level fluctuations but is considered sensitive to drainage and is therefore commonly regarded as an indicator of largely intact raised bog conditions. (Zechmeister, 1995)

Sphagnum angustifolium (Fig. 5.2) was likewise recorded in all site types but showed a distinctly different distribution pattern. In the open bog and bog forest, the species occurred regularly, mostly forming small patches (see Fig. 5.2 A) or appearing as scattered shoots within stands dominated by *S. magellanicum*. In the drained bog, *S. angustifolium* was primarily associated with former bog surfaces, where it locally formed small, monospecific stands. Its occurrence in drainage ditches was particularly notable,

Figure 5.2: Different situations of Sphagnum angustifolium. Small patch in open bog (A), mono-dominant manifestation in drainage ditches (B and C) (Own images)

as the species frequently dominated these habitats and often grew emergent from the water surface (see Fig. 5.2 B and C). *S. angustifolium* exhibits a comparatively broad ecological amplitude and is commonly described as an intermediate species between hummock and hollow taxa. Its tolerance of moderate shading and weakly mesotrophic conditions may explain its frequent occurrence in disturbed or hydrologically altered environments. (Daniels et al., 1985)

Sphagnum capillifolium (Fig. 5.3) was considerably less frequent within the study area. The species was recorded exclusively in the open bog and in a single bog forest plot, where it consistently occurred with very low cover. It was usually represented by only a few individuals embedded within lawns dominated by *S. magellanicum* (see Fig. 5.3 A). Plants displayed the characteristic green-red mottled (Fig. 5.3 B) to wine-red capitula (Fig. 5.3 A), particularly at sun-exposed sites.

Figure 5.3: Photos of Sphagnum capillifolium. A few wine-red specimens in a S. magellanicum carpet in the open bog (A) and a close-up of a green and red speckled shoot from the drained site (B) (Own images)

Despite its generally broad ecological amplitude, ranging from oligotrophic mires to open woodland, *S. capillifolium* played only a minor role within the investigated sites and contributed only marginally to the overall cover of the moss layer.

5.1.1.2. Forest mosses

All non-*Sphagnum* bryophytes are here referred to as forest mosses, following the functional distinction established in the theoretical framework (see Chapter 2.2.1.) to contrast peat-forming *Sphagnum* species with non-peat-forming bryophytes.

Forest mosses were largely restricted to forest-influenced and drained conditions and contributed only marginally to the vegetation of the open bog. Their occurrence and cover increased markedly in bog forest and drained bog plots, where they locally formed the most substantial component of the moss layer. The most prominent species were feathermosses such as *Pleurozium schreberi* (Fig. 5.4 A) and *Hylocomium splendens* (Fig.

Figure 5.4: Photos of the most common forest mosses in the study area. Pleurozium schreberi (A), Hylocomium splendens (B), Dicranum scoparium (C), and Rhytidiadelphus loreus (D) (Own images)

5.4 B), accompanied by other forest- and disturbance-associated bryophytes including *Dicranum scoparium* (Fig. 5.4 C) and *Rhytidiadelphus loreus* (Fig. 5.4 D). These species frequently formed carpets or patchy mats, whereas additional bryophytes occurred only sporadically and with low cover.

Within the drained bog, forest mosses were most pronounced on relatively dry and structurally stable surfaces, while their contribution remained low in waterlogged microhabitats. In contrast, intact open bog plots were characterized by an almost complete absence of forest mosses, with only isolated individuals of a few species recorded.

Overall, forest mosses represented a non-peat-forming bryophyte assemblage closely associated with shaded, drained, or structurally altered conditions, contrasting sharply with the dominance of peat-forming *Sphagnum* species in intact open bog vegetation.

5.1.2. Vascular plants

The vascular plant layers comprised a limited number of species characteristic of raised bogs, bog forests, and drained or disturbed peatland conditions. Typical species of active raised bogs (see Fig. 5.5) included *Andromeda polifolia*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*, and *Vaccinium uliginosum*. These species were primarily associated with open bog conditions and represent characteristic elements of oligotrophic, acidic peatlands.

Figure 5.5: Photos of characteristic species of active raised bogs. Flowering Andromeda polifolia (A), Eriophorum vaginatum with its eponymous seed head (B), Vaccinium oxycoccos with berries (C), and Vaccinium uliginosum with flowers (D) (Own images)

Several vascular plant species that occurred in the study area are commonly regarded as indicators of disturbance or successional change in raised bogs. These included *Molinia caerulea*, *Calluna vulgaris*,

Figure 5.6: Photos of indicator species for disturbances of active raised bogs. Molinia caerulea in August (A), flowering Calluna vulgaris (B) and Vaccinium myrtillus with berries (C) (Own images)

Vaccinium myrtillus (see Fig. 5.6), as well as tree species such as *Betula* spp., *Picea abies*, and *Pinus sylvestris*. *Frangula alnus* was of particular relevance, occurring frequently in bog forest and drained bog plots and only sporadically in the open bog.

Tree layers were dominated by acid-tolerant species typical of bog forests and drained sites, notably *Picea abies* (Fig. 5.7 A), which was the most prominent tree species, accompanied by *Betula pendula*, *Betula pubescens*, and *Pinus sylvestris* (Fig. 5.7 B to D). These species were consistently present in bog forest and drained bog plots and occurred only occasionally as isolated individuals in the open bog.

Figure 5.7: Photos of young individuals of the dominant tree species. Picea abies in open bog (A), Betula pendula in drained site (B), Betula pubescens (C) and Pinus sylvestris in open bog (D) (Own images)

The shrub layer was comparatively species-poor. *Frangula alnus* (Fig. 5.8) represented the most important shrub species, being common in bog forest and drained bog plots and rare in the open bog. *Sorbus aucuparia* was recorded only sporadically and with low abundance.

Within the herb layer, *Eriophorum vaginatum* and *Molinia caerulea* were among the most frequent species in the open bog, together with *Andromeda polifolia*, *Vaccinium oxycoccos*, and *Vaccinium uliginosum*. In contrast, *Vaccinium myrtillus* and *Molinia caerulea* were particularly prominent in bog forest and drained bog plots, where *V. myrtillus* represented the dominant species of the shrub layer.

Figure 5.8: Photo of Frangula alnus in one of the open bog plots (Own image)

Generally, the vascular plant assemblage reflected a gradient from typical raised bog species towards forest- and disturbance-associated taxa, with bog forest and drained bog plots characterized by a higher contribution of woody species and disturbance-tolerant graminoids.

5.2. Vegetation composition of site types and drainage features

Following the floristic overview, this section provides a detailed description of the vegetation composition of the investigated site types and drainage-related features. The open bog, bog forest, and drained bog sites are characterized in terms of species composition, dominant taxa, and the relative importance of different vegetation layers. Within the drained bog, vegetation patterns are further differentiated between mounts, former bog surfaces, and drainage ditches. In addition to species composition, structural aspects such as growth form dominance, tree cover, and moss layer development are described to provide a comprehensive picture of vegetation patterns across the study area. An overview of the identified species and their mean cover across the three site types is provided in Table 5.2.

Table 5.2: Frequency in study plots and mean coverage of plant species by site; typical species for intact raised bogs (according to Ellmauer and Traxler, 2001) are marked in light green

Frequency and coverage of plant species by study site								
Open bog			**Bog forest**			**Drained bog**		
Species	Frequenzy [x of 10 plots]	Mean cover [%]	Species	Frequenzy [x of 10 plots]	Mean cover [%]	Species	Frequenzy [x of 21 plots]	Mean cover [%]
Andromeda polifolia	9	3.73	Acer pseudoplatanus	1	0.01	Bazzania trilobata	1	0.71
Aulacomnium palustre	2	0.10	Aulacomnium palustre	2	0.10	Betula pendula	4	5.00
Betula pendula	1	0.01	Betula pendula	1	6.25	Betula pubescens	9	6.58
Betula pubescens	2	0.06	Betula pubescens	3	8.00	Carex rostrata	1	0.71
Calluna vulgaris	7	7.23	Dicranum scoparium	6	2.35	Dicranella heteromalla	3	0.07
Eriophorum vaginatum	10	19.10	Frangula alnus	8	5.62	Dicranum scoparium	13	1.95
Frangula alnus	2	0.16	Hylocomium splendens	4	2.85	Dryopteris dilatata	1	0.24
Melampyrum pratense	7	0.63	Molinia caerulea	10	20.40	Dryopteris expansa	2	0.12
Molinia caerulea	9	8.75	Picea abies	10	50.51	Eriophorum vaginatum	3	0.98
Picea abies	3	4.50	Pinus sylvestris	2	3.80	Fagus sylvatica	1	0.00
Pinus mugo	1	3.75	Plagiochila asplenioides	2	1.51	Frangula alnus	8	1.15
Pinus sylvestris	2	0.51	Pleurozium schreberi	10	21.05	Hylocomium splendens	7	4.88
Pleurozium schreberi	1	0.05	Rhytidiadelphus loreus	3	1.80	Leucobryum glaucum	2	0.05
Sphagnum angustifolium	10	38.00	Sorbus aucuparia	1	0.38	Molinia caerulea	12	10.71
Sphagnum capillifolium	6	2.35	Sphagnum angustifolium	9	12.05	Picea abies	13	32.58
Sphagnum magellanicum	10	45.75	Sphagnum capillifolium	1	0.05	Pinus sylvestris	5	6.07
Vaccinium myrtillus	6	9.60	Sphagnum magellanicum	9	29.50	Plagiomnium ellipticum	1	0.02
Vaccinium oxycoccos	10	6.78	Vaccinium myrtillus	10	26.75	Plagiomnium undulatum	1	0.02
Vaccinium uliginosum	1	2.50	Vaccinium vitis-idaea	1	0.25	Plagiothecium undulatum	1	0.12
						Pleurozium schreberi	17	17.79
						Polytrichum formosum	6	0.33
						Quercus robur	4	0.02
						Rhytidiadelphus loreus	12	4.21
						Sorbus aucuparia	2	0.24
						Sphagnum angustifolium	14	26.71
						Sphagnum magellanicum	12	16.55
						Syntrichia ruralis	1	0.00
						Vaccinium myrtillus	18	21.93

5.2.1. The open bog site

The open bog reference site was characterized predominantly by lawn microtopography, locally interspersed with low hummocks rising approximately 10-30 cm above the otherwise relatively even surface. During both sampling campaigns in May and August, surface conditions were consistently described as moist to wet. Although scattered trees occurred within the open bog (see Fig. 5.9), overall tree cover was very low, and individuals frequently exhibited growth limitations associated with wet site conditions. In addition to a few taller trees, several individuals were reduced in stature and assigned to the shrub or even herb layer. The most common tree species was *Picea abies*, followed by *Pinus sylvestris* and *Betula pubescens*; a single individual of *Betula pendula* was recorded within the shrub layer.

Figure 5.9: View into the open bog in May (Own image)

Figure 5.10: Open bog plot B1 in August as an example of the composition of the herb and moss layer. Sphagnum mosses, Eriophorum vaginatum, Calluna vulgaris, and some Vaccinium myrtillus are apparent (Own image)

Vegetation of the open bog was clearly dominated by *Sphagnum* species (visible in Fig. 5.10). Among the three identified taxa, *Sphagnum magellanicum* exhibited the highest mean cover, accounting for roughly 45 % of the surface area and occurring in all sampled plots (see Tab. 5.2). *Sphagnum angustifolium* was likewise present in all plots and reached similarly high cover values, averaging close to 40 %. *Sphagnum capillifolium* was detected in more than half of the plots, but only as scattered individuals, contributing marginally to overall cover (approximately 2 %). Other bryophytes were rare; only the forest mosses *Aulacomnium palustre* and *Pleurozium schreberi* occurred sporadically and with very low cover.

The herb layer of the open bog supported several species typical of active raised bogs. *Eriophorum vaginatum* was a prominent component of the vegetation, covering roughly one fifth of the sampled area and representing a defining structural element of the site (see Fig. 5.10 and 5.11). *Vaccinium oxycoccos* and *Andromeda polifolia* were recorded with high frequency but generally low cover. *Vaccinium*

Figure 5.11: White seed stands of Eriophorum vaginatum in the open bog situation of May (Own image)

uliginosum, another species indicative of intact raised bog conditions, formed locally larger stands, although only one plot was located within these patches (see. Tab. 5.2). Additional species commonly associated with raised bogs, but often regarded as disturbance or transitional indicators, included *Molinia caerulea*, which occurred in nine out of ten plots with an average cover of approximately 9 %, as well as *Calluna vulgaris* and *Vaccinium myrtillus (see Fig. 5.10)*. The latter increased in dominance towards the margins of the open bog area.
The shrub layer was consistently weakly developed. Apart from juvenile individuals of tree species, *Frangula alnus* was recorded in only two plots and with very low cover. *Pinus mugo* was detected in a single plot (see Tab. 5.2) and contributed only marginally to vegetation cover within the sampled area; however, this species was observed to be strongly dominant in other parts of the bog complex not included in the present survey.

5.2.2. The bog forest site

The bog forest reference site was characterized by predominantly level terrain, locally interrupted by small hummocks and overgrown tree stumps. Surface conditions at the sampled plots were generally described as moist, with locally wet patches recorded during both sampling periods. The site was clearly shaped by forest cover (see Fig. 5.12), ranging from relatively open to locally dense stands. Estimated canopy cover across plots varied widely, from approximately 20 % to over 90 %, with an average canopy cover of around 65 %.

Figure 5.12: Situation of the bog forest plot T2 in May as an example of the composition and structure of the site (Own image)

The tree layer was strongly dominated by *Picea abies*, which occurred in all sampled plots and accounted for approximately half of the total tree cover (see Tab. 5.2). Additional tree species included *Betula pubescens*, *Pinus sylvestris*, and *Betula pendula*, which were present at lower frequencies and generally contributed only minor proportions to total cover.

The moss layer was dominated by a small number of bryophyte species with high frequency and substantial cover. *Sphagnum magellanicum* was a consistent component of the moss layer, reaching mean cover values of approximately 30 %. In addition, *Pleurozium schreberi* formed extensive carpets in many plots and contributed on average slightly more than 20 % cover. *Sphagnum angustifolium* was also regularly recorded, with mean cover values around 10-15 %. Other bryophyte species, including *Dicranum scoparium*, *Hylocomium splendens*, and *Rhytidiadelphus loreus*, occurred less frequently and typically with low cover, generally not exceeding a few percent. Additional species such as *Plagiochila asplenioides*, *Aulacomnium palustre*, and *Sphagnum capillifolium* were recorded only sporadically and with very low cover.

The herb layer of the bog forest showed considerable variation among plots, ranging from weakly to strongly developed. It was largely composed of two species that occurred with high frequency and comparatively high cover (see Fig. 5.13). *Vaccinium myrtillus* was present in all plots and reached mean cover values of approximately 25-30 %, while *Molinia caerulea* occurred with similarly high frequency and an average cover of about 20 %. Apart from these dominant species, the herb layer contained only few additional taxa, including isolated individuals of *Vaccinium vitis-idaea* and juvenile tree seedlings, most notably *Acer pseudoplatanus* and *Picea abies*, each recorded in a single plot.


Figure 5.13: Well-developed herb layer with Vaccinium myrtillus and Molinia caerulea in plot T1 of the bog forest site (August) (Own image)

The shrub layer was generally species-poor and varied in development among plots. *Frangula alnus* represented the most consistent shrub species, occurring in several plots but contributing only low mean cover values of around 5 %. Aside from a single juvenile individual of *Picea abies*, *Sorbus aucuparia* was recorded in only one plot and with very low cover.

5.2.3. The drained bog site

Within the drained bog site, vegetation composition differed primarily among the three drainage-related features considered, namely mounts, former surfaces, and drainage ditches. Species composition and dominance patterns of the different drainage-related features are shown in Table 5.3. The most pronounced contrasts were observed between the drainage ditches and the two remaining feature types, mounts and former surfaces, which showed more similar vegetation characteristics. In contrast, the composition of the tree layer was largely comparable across all features and is therefore described jointly.

Table 5.3: Frequency in study plots and mean coverage of plant species in the drained bog study site by terrain feature; typical species for intact raised bogs (according to Ellmauer and Traxler, 2001) are marked in light green

Frequency and coverage of plant species in the drained bog site by terrain feature								
Mount			**Former surface**			**Drainage ditch**		
Species	Frequenzy [x of 8 plots]	Mean cover [%]	Species	Frequenzy [x of 8 plots]	Mean cover [%]	Species	Frequenzy [x of 5 plots]	Mean cover [%]
Bazzania trilobata	1	1.88	Betula pendula	2	0.33	Carex rostrata	1	3.00
Betula pendula	2	12.81	Betula pubescens	4	9.06	Dryopteris expansa	1	0.50
Betula pubescens	5	8.20	Dicranella heteromalla	2	0.13	Eriophorum vaginatum	2	4.10
Dicranella heteromalla	1	0.06	Dicranum scoparium	5	1.31	Hylocomium splendens	1	0.50
Dicranum scoparium	8	3.81	Eriophorum vaginatum	1	0.01	Molinia caerulea	2	2.05
Dryopteris dilatata	1	0.63	Fagus sylvatica	1	0.01	Pleurozium schreberi	1	0.10
Dryopteris expansa	1	0.01	Frangula alnus	5	2.58	Polytrichum formosum	1	0.10
Frangula alnus	3	0.44	Hylocomium splendens	3	1.25	Quercus robur	1	0.02
Hylocomium splendens	3	11.25	Leucobryum glaucum	1	0.06	Sphagnum angustifolium	5	77.50
Leucobryum glaucum	1	0.06	Molinia caerulea	6	20.03	Sphagnum magellanicum	2	10.50
Molinia caerulea	4	6.81	Picea abies	7	33.59	Vaccinium myrtillus	2	3.10
Picea abies	6	51.94	Pinus sylvestris	4	12.81			
Pinus sylvestris	1	3.13	Plagiomnium ellipticum	1	0.06			
Plagiomnium undulatum	1	0.06	Plagiothecium undulatum	1	0.31			
Pleurozium schreberi	8	33.13	Pleurozium schreberi	8	13.50			
Polytrichum formosum	4	0.75	Polytrichum formosum	1	0.06			
Quercus robur	2	0.03	Quercus robur	1	0.01			
Rhytidiadelphus loreus	8	10.31	Rhytidiadelphus loreus	4	0.75			
Sorbus aucuparia	1	0.31	Sorbus aucuparia	1	0.31			
Sphagnum angustifolium	2	3.44	Sphagnum angustifolium	7	18.25			
Sphagnum magellanicum	3	6.56	Sphagnum magellanicum	7	30.31			
Syntrichia ruralis	1	0.01	Vaccinium myrtillus	8	24.22			
Vaccinium myrtillus	8	31.41						

Figure 5.14: Forest situation in May around plot F5 of the drained site, with visible differences in crown density and understory development (Own image)

Overall tree cover within the drained bog averaged approximately 50 %, although canopy density varied markedly among plots (see example in Fig. 5.14). In plots with low or absent canopy cover, a dense understory of juvenile trees was frequently present. Due to their limited height, these individuals were assigned to the shrub layer. The tree layer was dominated by *Picea abies*, which exhibited the highest frequency and cover across all features, followed by *Betula pendula*. *Betula pubescens* and *Pinus sylvestris* were also recorded in several plots but contributed substantially lower cover values (see Appendix D).

In the following sections, vegetation composition of the drained bog is described separately for mounts, former surfaces, and drainage ditches in order to highlight feature-specific differences in species composition and structural characteristics.

5.2.3.1. Mount features

Mount features were located on the excavated peat heaps adjacent to drainage ditches. The sampled plots were generally flat to slightly uneven and locally inclined. Surface conditions were described as dry to slightly moist during both sampling periods.

The moss layer on mounts was well developed and characterized by a comparatively high number of bryophyte species, most of which occurred only sporadically and with low cover. These included, in decreasing order of abundance, *Bazzania trilobata*, *Dicranella heteromalla*, *Leucobryum glaucum*, *Plagiomnium undulatum*, and *Syntrichia ruralis*. In contrast, several forest moss species were consistently present across all plots. *Pleurozium schreberi* was the dominant bryophyte, reaching mean cover values of approximately 30 %. It was accompanied by *Rhytidiadelphus loreus* (around 10 % cover) and *Dicranum scoparium* (approximately 4 %). *Hylocomium splendens* occurred with lower frequency but locally reached cover values of around 10 %, whereas *Polytrichum formosum* was present only sporadically and with low cover. Typical raised bog species were represented by *Sphagnum magellanicum* and *S. angustifolium*, both occurring at low to moderate cover.

Figure 5.15: Comparison between plots M1 and M7 in the drained site, with a noticeable difference in shrub and herb layer density (Own image)

The herb layer on mount features varied considerably among plots, largely depending on light availability (see as an example Fig. 5.15). Overall, it was clearly dominated by *Vaccinium myrtillus*, which occurred in all plots and reached mean cover values of approximately 30 %. *Molinia caerulea* was present in about half of the plots with moderate cover. Other herbaceous species were rare and included the ferns *Dryopteris dilatata* and *Dryopteris expansa*, each recorded in a single plot, as well as juvenile individuals of *Picea abies* and *Quercus robur*.

Development of the shrub layer was likewise heterogeneous and closely related to canopy density (see Fig. 5.15). In plots with low or absent tree cover, dense regeneration of *Picea abies* and, to a lesser extent, *Betula pubescens* was recorded, although these individuals were assigned to the shrub layer due to their limited height. Under more shaded conditions, the shrub layer was dominated by *Frangula alnus*, occasionally accompanied by *Sorbus aucuparia*, both generally contributing less than 1% cover.

5.2.3.2. Former surface features

Former surface features represent areas of the drained bog that correspond to the former raised bog surface and were not directly altered by excavation or peat displacement. As exemplified in Figure 5.16, the sampled plots were generally level, with only few minor surface irregularities. Surface conditions were assessed as dry to moderately moist during both sampling periods.

Figure 5.16: Situation around plot F8 in drained bog in dense forest with no shrub layer but well-developed herb and moss layer (Own image)

The moss layer was well developed and dominated by a small number of bryophyte species with high frequency and substantial cover. *Sphagnum magellanicum* was the most prominent species (see Fig. 5.17), reaching mean cover values of approximately 30 %. It was accompanied by *Sphagnum angustifolium*, which contributed around 20 % cover on average. In addition, the forest moss *Pleurozium schreberi* formed an important component of the moss layer, with mean cover values of roughly 10-15 %. Other bryophytes, including *Dicranum scoparium*, *Rhytidiadelphus loreus*, and *Hylocomium splendens*, occurred with lower frequency and generally low cover, typically around 1 %. Further species such as *Dicranella heteromalla*, *Plagiothecium undulatum*, *Leucobryum glaucum*, *Plagiomnium ellipticum*, and *Polytrichum formosum* were recorded only sporadically and with very low abundance.

Figure 5.17: Photo of plot F5 in May, with Vaccinium myrtillus and Molinia caerulea in the shrub layer and a moss layer dominated by Sphagnum magellanicum (Own image)

The herb layer of the former surface features varied considerably among plots, ranging from weakly to strongly developed depending on local light conditions. *Vaccinium myrtillus* was present in all plots (see Fig. 5.17) and dominated the herb layer with mean cover values of approximately 25 %. *Molinia caerulea* (see also Fig. 5.17) was also frequent, occurring in most plots and reaching average cover values of around 20 %. The typical raised bog species *Eriophorum vaginatum* was recorded in one plot only and contributed negligible cover. Additional herbaceous species included juvenile individuals of *Picea abies*, *Fagus sylvatica*, and *Quercus robur*.

The shrub layer was generally weakly developed and was absent from several plots. *Frangula alnus* represented the most consistent shrub species, occurring with relatively high frequency but contributing only low mean cover values of around 3 %. Occasional small individuals of *Betula pendula* and *Betula pubescens* were recorded, while *Sorbus aucuparia* was observed in a single plot only.

5.2.3.3. Drainage ditch features

Drainage ditch features comprised the variable-width bottoms of actively draining ditches (see Fig. 5.18 and 5.19). During both sampling periods standing water several decimeters deep was present across large parts of the plots. A floating moss layer covered much of the water surface (see Fig. 5.18), while comparatively drier microsites occurred locally along the ditch margins. In some plots, steep ditch banks were partially included within the 1 x 1 m sampling areas, resulting in the recording of species extending from adjacent, less waterlogged habitats.

Figure 5.18: Photo of a drainage ditch dominated by Sphagnum angustifolium at the drained bog site in May (Own image)

The vegetation of the drainage ditches was characterized by an almost continuous moss layer, which was formed predominantly by *Sphagnum* species. *Sphagnum angustifolium* was by far the most abundant species, occurring in all sampled plots and covering, on average, more than three quarters of the plot surface. This species primarily occupied the permanently flooded sections of the ditches, as shown in Figure 5.18. *Sphagnum magellanicum* was recorded at slightly elevated microsites above the water surface in two plots and contributed only moderate cover. Other bryophytes, including *Hylocomium splendens*, *Pleurozium schreberi*, and *Polytrichum formosum*, were detected only sporadically on steep ditch banks and exhibited very low cover values.

Figure 5.19: Photo of plot D2 in a wide drainage ditch with Sphagnum angustifolium, Carex rostrata, and Eriophorum vaginatum (Own image)

The herb layer was generally sparse but included several hydrophilic and raised-bog-associated species (see as an example Fig. 5.19). *Eriophorum vaginatum* and *Molinia caerulea* were recorded with low frequency and low cover (>5 %), additionally *Carex rostrata* occurred locally and reached similar cover values. At comparatively drier ditch margins, *Vaccinium myrtillus* was present with low cover, occasionally accompanied by *Dryopteris expansa* and isolated seedlings of *Quercus robur*. A shrub layer was absent from all drainage ditch plots.

5.3. Species richness and seasonal variation

This section summarizes seasonal changes in vegetation between the May and August surveys and examines patterns of species richness across site types and drainage-related features.

5.3.1. Seasonal variation

For the majority of species, no changes in presence or absence were observed between the May and August surveys, and overall species composition remained largely stable. Seasonal differences were mainly expressed as changes in cover of species already present within the plots, rather than through the appearance of new species or the expansion into previously unoccupied plots.

In the open bog, the mean cover of *Molinia caerulea* increased markedly from spring to late summer, while the cover of *Eriophorum vaginatum* decreased between the two surveys. A slight reduction in mean cover was also observed for *Andromeda polifolia*. In the bog forest, seasonal changes were particularly pronounced for *Vaccinium myrtillus*, whose mean cover decreased substantially from May to August, whereas *Molinia caerulea* showed a strong increase in cover over the same period. Similar patterns were observed within the drained bog. On mounts and former surfaces, as shown in exemplary Figure 5.20, *Vaccinium myrtillus* exhibited a pronounced decline in mean cover from spring to late summer, while *Molinia caerulea* increased in abundance. Within drainage ditches, increases in the cover of *Molinia caerulea* and *Eriophorum vaginatum* were recorded between the two surveys.

Figure 5.20: Visible change in the coverage of Vaccinium myrtillus and Molinia caerulea between May (left) and August (right) in plot F6 in the drained bog (Own images)

Despite these shifts in cover, species richness did not differ significantly between the May and August surveys (paired Wilcoxon signed-rank test, $V = 3$, $p = 0.35$). Likewise, overall species composition showed no significant seasonal differences (PERMANOVA based on Bray-Curtis dissimilarity: $F_{1,80} = 1.03$, $R^2 = 0.013$, $p = 0.365$). Seasonal variation was therefore considered negligible with respect to species presence and overall community composition, and data from both surveys were pooled for all subsequent analyses.

5.3.2. Species richness across site types

Species richness per plot varied within a comparable range across all investigated site types (Fig. 5.21). Median species richness was highest in the open bog (median = 10 species per plot, range = 7-12), followed by the bog forest (median = 9, range = 8-12) and the drained bog (median = 9, range = 1-13). Mean values showed a similar pattern, with averages of 9.9 species per plot in the open bog, 9.3 in the bog forest, and 8.3 in the drained bog.

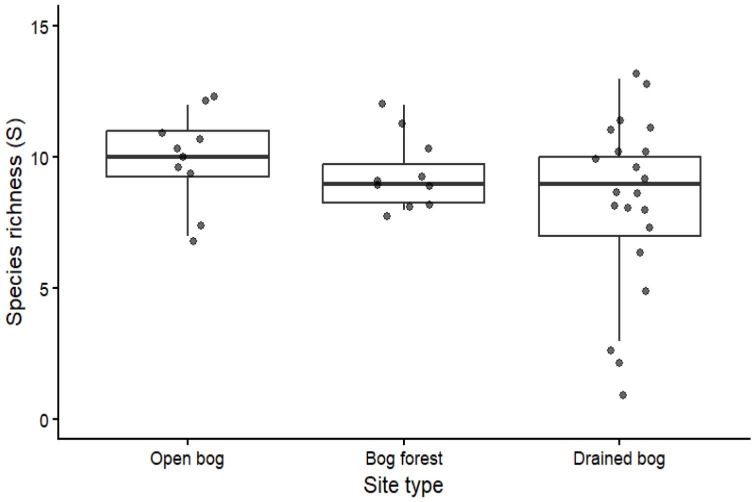

Figure 5.21: Species richness per plot across the three site types (open bog, bog forest, and drained bog). Boxplots show median values, interquartile ranges, and minimum–maximum ranges based on pooled data from the May and August surveys

Despite these differences in central tendency and spread, total species richness did not differ significantly among site types (Kruskal-Wallis test, $x^2 = 2.04$, *df* = 2, $p = 0.36$). Pairwise comparisons likewise revealed no significant differences between individual site types (Holm-adjusted Wilcoxon tests, $p > 0.5$ for all comparisons). Notably, plots from the drained bog exhibited the widest range of species richness values, reflecting a high variability in local site conditions.

5.3.3. Species richness within the drained bog

Within the drained bog, species richness differed significantly among drainage-related features (Kruskal-Wallis test, $p = 0.007$; Fig. 5.22). Drainage ditches showed markedly lower species richness than the other feature types, with a median of 3 species per plot (range = 1-8, mean = 3.8). In contrast, former surfaces and mounts exhibited substantially higher richness values. Median species richness was 10 species per plot on former surfaces (range = 7-13, mean = 8.0) and 9 species per plot on mount features (range = 6-13, mean = 9.4).

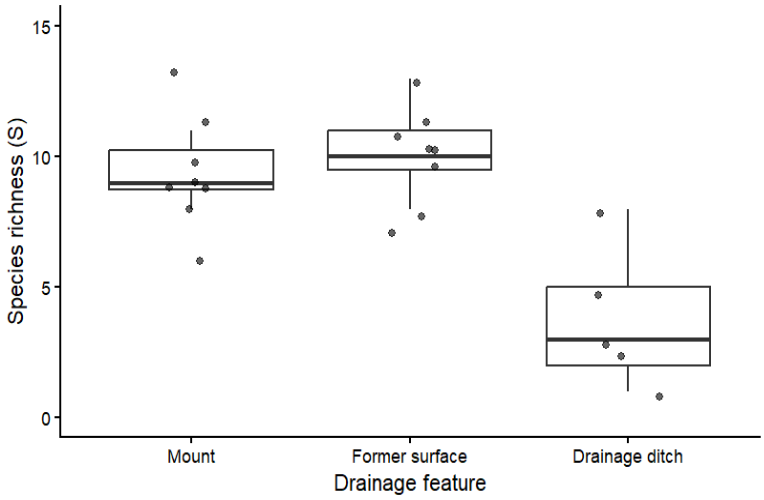

Figure 5.22: Species richness per plot across drainage-related features within the drained bog (mounts, former surfaces, and drainage ditches). Boxplots represent median species richness, interquartile ranges, and minimum–maximum values based on pooled data from both sampling seasons

Post-hoc pairwise comparisons confirmed that species richness in drainage ditches was significantly lower than on both former surfaces and mounts (Holm-adjusted Wilcoxon tests, $p = 0.024$ in both cases), whereas no significant difference was detected between former surfaces and mounts ($p = 0.46$). These patterns are reflected in the boxplots by a clearly separated lower median and reduced interquartile range for drainage ditches.

5.3.4. Contribution of bryophytes and vascular plants

The relative contribution of bryophytes and vascular plants to total species richness differed among site types (Fig. 5.23 A). In the open bog, vascular plants exhibited a higher mean species richness per plot (mean = 7.0, median = 7.5) than bryophytes (mean = 2.9, median = 3.0), reflecting the presence of several characteristic dwarf shrubs and graminoids alongside a comparatively small number of highly specialized bryophyte species.

In contrast, bog forest and drained bog plots showed a more balanced contribution of bryophytes and vascular plants. In the bog forest, mean species richness of bryophytes (mean = 4.6, median = 4.5) and vascular plants (mean = 4.7, median = 5.0) were similar. A comparable pattern was observed in the drained bog, where mean richness values of bryophytes (mean = 4.3, median = 5.0) and vascular plants (mean = 4.4, median = 5.0) were nearly equal.

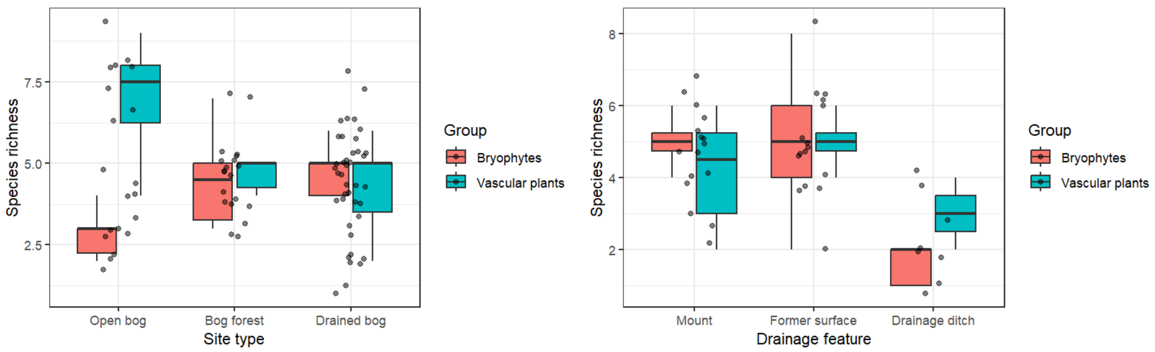

Figure 5.23: Species richness of bryophytes and vascular plants per plot across site types (A) and drainage-related features within the drained bog (B). Boxplots illustrate the distribution of species richness per plot for each taxonomic group (bryophytes and vascular plants) in open bog, bog forest, and drained bog sites, as well as mounts, former surfaces, and drainage ditches

Within the drained bog, differences among drainage features were also evident when species richness was separated by taxonomic group (Fig. 5.23 B). Mounts and former surfaces supported higher bryophyte richness (median = 5 species per plot for both features) than drainage ditches (median = 2). Vascular plant richness showed a similar, though less pronounced, pattern, with lowest median values recorded in drainage ditches (median = 3), compared to mounts (median = 4.5) and former surfaces (median = 5).

5.4. Vegetation classification

5.4.1. Plant community assignment

The vegetation of the investigated site types was assigned to higher-ranked plant community units based on a synoptic comparison of species composition, dominance patterns, and structural characteristics, following the diagnostic species concepts described by Steiner (1992) and presented under Chapter 3.2.3. Given the transitional character of the study area and the influence of drainage and forest encroachment, no formal plot-based classification was applied. Instead, community affinities were evaluated at the level of site types, supported by indicator species analysis. The classification of vegetation types was carried out on the basis of characteristic combinations of species, their constancy, and mean cover across site types (see Tab. 5.2).

5.4.1.1. Open bog

The vegetation of the open bog site can be assigned to ombrotrophic raised bog communities of the class *Oxycocco-Sphagnetea* and the order *Sphagnetalia magellanici*. This assignment is supported by the presence of numerous characteristic species of oligotrophic raised bogs typical of boreal and temperate regions, including *Vaccinium oxycoccos*, *Eriophorum vaginatum*, *Andromeda polifolia*, *Vaccinium uliginosum*, and peat-forming *Sphagnum* species.

Within this order, the species composition shows a close affinity to the alliance *Sphagnion magellanici*, which comprises raised bog hummock communities of the temperate zone. As the vegetation structure of the open bog is dominated by *Sphagnum* lawns and low hummocks, accompanied by ericaceous dwarf shrubs and oligotrophic graminoids, it corresponds well to the physiognomy described for this alliance.

The highest floristic agreement is observed with the association *Sphagnetum magellanici*, a largely treeless raised bog community typical of middle and higher elevations of the Central European mountains. In addition to the dominant *Sphagnum magellanicum*, the presence of *S. capillifolium*, *S. angustifolium*, *Polytrichum strictum*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*, *V. uliginosum*, and *Andromeda polifolia* corresponds closely to the differential species combination described for this association by Steiner (1992).

Although scattered individuals of *Picea abies* occurred within the open bog, these stands are best interpreted as a structural variant of the *Sphagnetum magellanici*, as described by Steiner (1992), rather than representing a distinct syntaxonomic unit. Shading remained low, and the characteristic species composition of the moss and dwarf-shrub layers was largely unaffected.

In one plot, *Pinus mugo* was recorded with low cover, and extensive stands of this species occur outside the sampled area. This indicates local affinities to the association *Pino mugo-Sphagnetum magellanici*, which is defined by the presence of *Pinus mugo* on drier raised bog hummocks. However, within the investigated plots, this association is only weakly expressed.

Indicator species analysis strongly supported the distinctiveness of the open bog vegetation, identifying *Vaccinium oxycoccos*, *Eriophorum vaginatum*, *Andromeda polifolia*, and several *Sphagnum* species as significant indicators for this site type.

5.4.1.2. Bog forest

The bog forest site represents a transitional vegetation type between open raised bog communities and coniferous forest vegetation. Floristically and structurally, the vegetation can be assigned to the class *Vaccinio-Piceetea* and the order *Vaccinio-Piceetalia*, which typically occupy weakly minerotrophic bog margins and function as transition zones between peatland and mineral-soil forests.

The species composition is characteristic of the alliance *Vaccinio-Piceion*, as indicated by the dominance of *Picea abies* in the tree layer, the high abundance of dwarf shrubs such as *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, and the frequent occurrence of forest mosses including *Pleurozium schreberi*, *Hylocomium splendens*, and *Dicranum scoparium*. The latter represents an important differential species within mire-margin spruce forests.

Among the associations described for this alliance, the vegetation of the bog forest site shows the closest correspondence to the *Bazzanio-Piceetum*, a spruce-dominated mire-margin forest community developing on dry peat soils. This assignment is supported by the frequent occurrence of *Picea abies* and *Dicranum scoparium*.

The comparatively high cover of *Sphagnum magellanicum* indicates affinities to the *Sphagnum magellanicum* subunit of the *Bazzanio-Piceetum*, which represents a transitional form toward spruce-dominated expressions of the *Sphagnetum magellanici*. These stands are characterized by denser and taller spruce canopies than in open bog woodland, resulting in patchier *Sphagnum* layers and altered light conditions.

Indicator species analysis further supported this classification by identifying *Frangula alnus*, *Picea abies*, *Pleurozium schreberi*, and *Molinia caerulea* as significant indicators of the bog forest site type.

5.4.1.3. Drained bog

The vegetation of the drained bog site is characterized by pronounced structural and floristic heterogeneity resulting from drainage and microtopographic differentiation. Despite this heterogeneity, the overall species composition indicates a clear affinity to mire-margin and forest-related communities of the class *Vaccinio-Piceetea*, order *Vaccinio-Piceetalia*, and alliance *Vaccinio-Piceion*.

Similar to the bog forest, the drained bog vegetation is dominated by *Picea abies* in the tree layer and by dwarf shrubs such as *Vaccinium myrtillus* and shrubs like *Frangula alnus* in the understory. Forest mosses including *Pleurozium schreberi*, *Hylocomium splendens*, and *Dicranum scoparium* are widespread, reflecting increased aeration and reduced water saturation of the peat substrate.

Among the considered associations, the drained bog shows the highest correspondence with the *Bazzanio-Piceetum*. In addition to *Picea abies* and *Dicranum scoparium*, the characteristic liverwort *Bazzania trilobata* was recorded in one plot, further supporting this assignment. However, in contrast to the bog forest, the vegetation of the drained bog retains only scattered remnants of raised bog species, and *Sphagnum* cover is strongly reduced or spatially restricted.
Indicator species analysis yielded generally low indicator values for the drained bog site type, reflecting the absence of a coherent diagnostic species set and the dominance of successional and disturbance-related processes. The vegetation of the drained bog therefore represents degraded and structurally altered expressions of mire-margin spruce forest communities rather than a well-defined syntaxonomic unit.

5.4.2. Assignment to FFH Habitat types

Based on the floristic composition, dominance patterns, and vegetation structure described above, the investigated site types can be related to habitat types of Community interest according to Annex I of the Habitats Directive (92/43/EEC). This assignment follows the definitions and characteristic species outlined in Chapter 2.2.4 and is supported by species frequency and cover patterns presented in Section 5.2, as well as by the results of the indicator species analysis.

The investigated open bog site corresponds to habitat type 7120 - Degraded raised bogs still capable of natural regeneration. As the vegetation is dominated by peat-forming *Sphagnum* species, particularly *Sphagnum magellanicum* and *S. angustifolium*, accompanied by characteristic raised bog vascular plants such as *Eriophorum vaginatum*, *Vaccinium oxycoccos*, *Vaccinium uliginosum*, and *Andromeda polifolia*. This species combination is typical of ombrotrophic bog vegetation of the *Sphagnion magellanici* and closely resembles the association *Sphagnetum magellanici*. However, compared to intact active raised bogs (7110), the site shows signs of structural alteration, including the presence of scattered trees (*Picea abies*, *Betula spp.* and *Pinus sylvestris*) and an increased abundance of species such as *Calluna vulgaris*, *Molinia caerulea* and *Vaccinium myrtillus* in many of the sampled plots. These features are consistent with the definition of habitat type 7120, which encompasses degraded but still regenerable raised bog surfaces.

The bog forest site can be assigned to the priority habitat type 91D0 - Bog woodland.
The vegetation is characterized by a *Picea abies* -dominated canopy accompanied by other typical bog woodland tree species, such as *Betula spp*. and *Pinus sylestris*. Similarly, the well-developed ground layer is comprised of species described for this habitat type, including *Vaccinium myrtillus*, *Molinia caerulea* and *Vaccinio-Piceetea*-associated forest mosses like *Pleurozium schreberi*, *Dicranum scoparium*, and locally *Hylocomium splendens*. At the same time, peatland influence remains evident through the frequent occurrence of *Sphagnum magellanicum* and *S. angustifolium*.

This combination of forest and bog species corresponds closely to the alliance *Vaccinio-Piceion* and shows the highest floristic affinity to the association *Bazzanio-Piceetum*, which serves as an indication of its classification as habitat type 91D0.

Likewise, vegetation within the drained bog site also shows similarities to habitat type 91D0 - Bog woodland, although with pronounced spatial heterogeneity related to drainage-induced microtopography.
In addition to *Picea abies*, the two *Betula* species, and *Pinus sylvestris*, other typical species of this habitat type also occur in the tree layer. Despite the abundance of diverse forest moss species present in the moss layer, the presence of *Sphagnum angustifolium* and *Sph. magellanicum* persists, exhibiting substantial coverage. Together with the predominance of *Vaccinium myrtillus* and *Molinia caerulea*, these elements underscore the bog-like characteristics of this forest community.
The classification of this site as part of the alliance *Vaccinio-Piceion*, specifically the association *Bazzanio-Piceetum*, suggests a probable affiliation with habitat type 91D0.

5.5. Patterns in vegetation composition and environmental relationships

5.5.1. Environmental data

Environmental conditions differed markedly among the three site types investigated (Fig. 5.24; Appendix E). Mean topsoil water content was highest in the open bog (mean = 0.928 ± 0.015 SD) and slightly lower in the bog forest (0.896 ± 0.013), whereas the drained bog showed the lowest mean water content and the largest variability (0.851 ± 0.085) due to the differences in conditions between the investigated features. Peat decomposition (Von Post scale) in the upper layer of the soil increased from the open bog (mean = 2.8 ± 0.8) to the bog forest (5.6 ± 1.6) and reached the highest values in the drained bog (6.76 ± 2.68), consistent with a pronounced drainage-related decomposition gradient. Soil pH varied only slightly among site types, with mean values ranging from 3.29 to 3.48 and overlapping distributions in the boxplots (see Fig. 5.24). The estimated canopy density clearly separated the open bog from the forest-influenced site types, with very low mean canopy cover in the open bog (7.5 ± 14.0) compared to the bog forest (64.5 ± 29.7) and intermediate values in the drained bog (42.9 ± 29.2), reflecting substantial within-type heterogeneity in tree influence (Fig. 5.24).

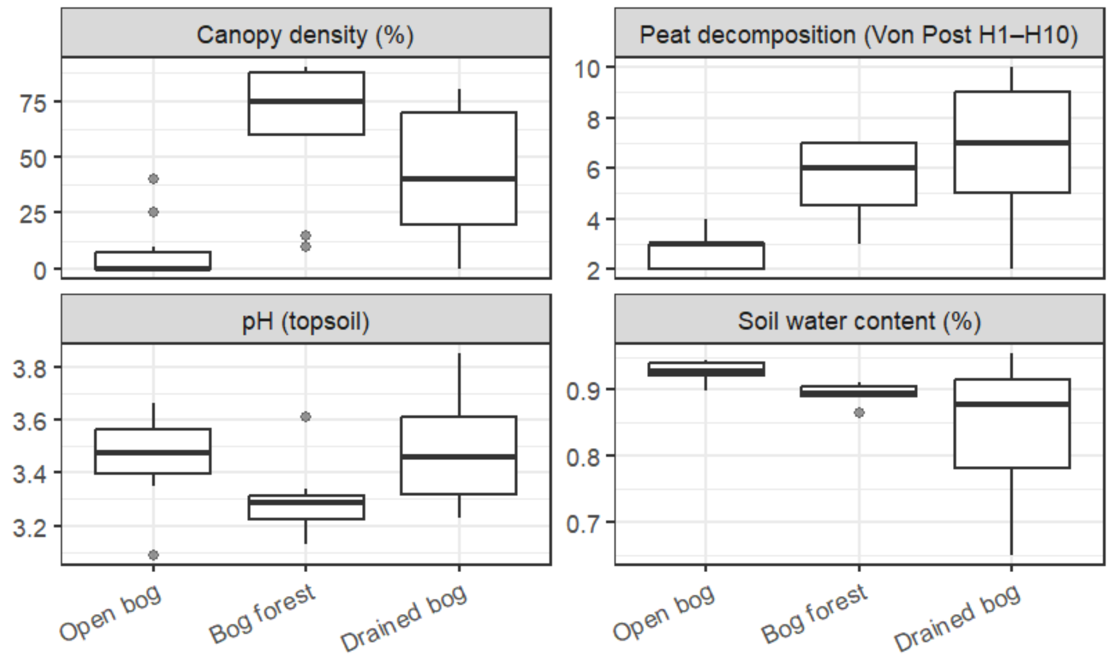

Figure 5.24: Boxplots of environmental variables by site type (open bog, bog forest, drained bog): topsoil water content (% of dry mass) and peat decomposition (Von Post), topsoil pH, and canopy density (% of cover). Boxes show median and interquartile range; whiskers indicate 1.5x IQR; points represent outliers

Within the drained bog, the drainage-related microtopographic features differed strongly in hydrological status and peat decomposition (Fig. 5.25). The water filled drainage ditches had as expected the highest mean water content (0.945 ± 0.008) and the lowest decomposition values (2.6 ± 0.55), whereas mounts reflected the driest and most decomposed conditions (water content 0.761 ± 0.052; decomposition 9.13 ± 0.83). Former surfaces were rather intermediate in water content (0.884 ± 0.030) but also showed higher decomposition (7.0 ± 0.93). Mean pH remained within a narrow acidic range across features (3.37-3.56), and canopy density varied widely within each feature category, with drainage ditch features showing the lowest mean tree covers (Fig. 5.25).

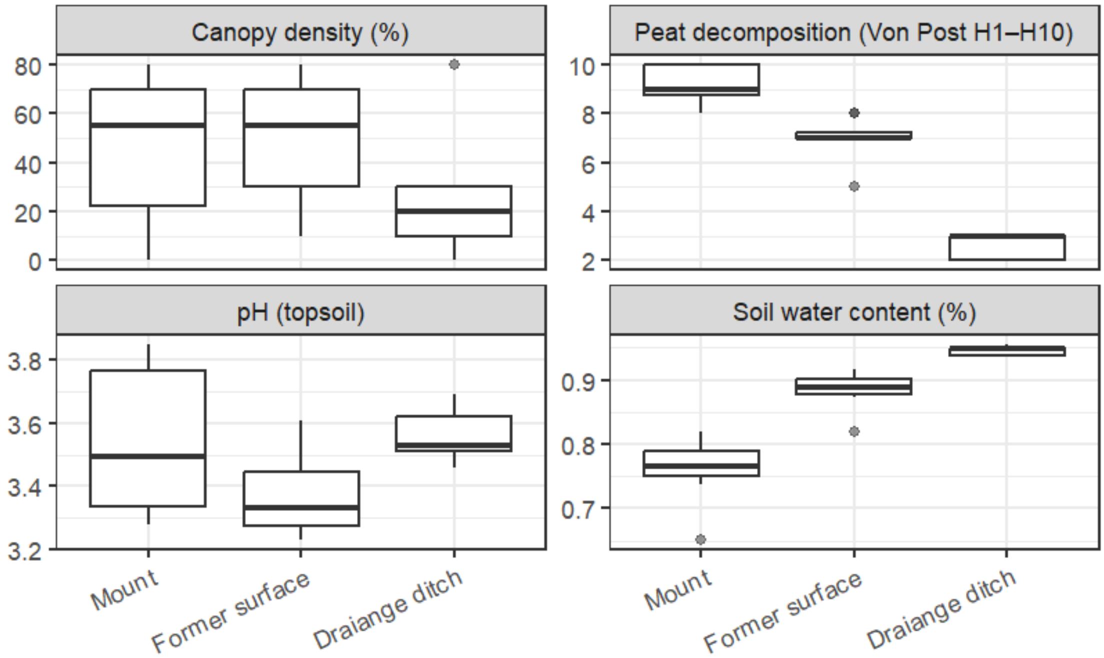

Figure 5.25: Boxplots of environmental variables within the drained bog by drainage-related microtopographic feature (mount, former surface, drainage ditch): topsoil water content (% of dry mass) and peat decomposition (Von Post), topsoil pH, and canopy density (% of cover). Boxes show median and interquartile range; whiskers indicate 1.5x IQR; points represent outliers

5.5.2. Multivariate patterns of vegetation composition and environmental drivers

Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities was used to visualize multivariate patterns in species composition among plots. The two-dimensional solution achieved an acceptable fit (stress = 0.147), indicating that the main compositional relationships were represented reasonably well in ordination space (Fig. 5.26).

Plots from the open bog formed a compact cluster in the ordination space, clearly separated from the majority of drained bog plots, while bog forest plots occupied an intermediate position and partly overlapped with the drained bog cluster (Fig. 5.26). Within the drained bog, drainage ditches were mainly located at the wetter end of the ordination space, whereas mounts were positioned towards the drier and more strongly decomposed part of the gradient. Former surface plots occupied intermediate positions and partly overlapped with both feature types (Fig. 5.26).

A PERMANOVA confirmed significant differences in species composition among the three site types (Bray-Curtis; adonis2: $F_{2,38} = 5.63$, $R^2 = 0.229$, $p = 0.001$). Site type therefore explained, with approximately 23 % a substantial proportion of variation in community composition, while remaining variability was attributable to within-type heterogeneity at the plot scale.

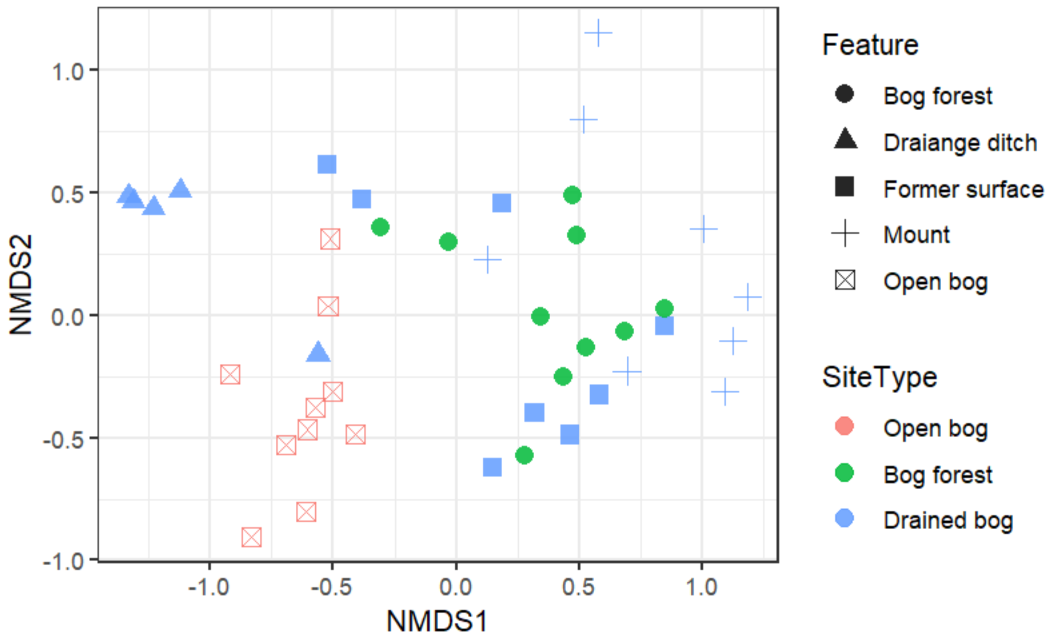

Figure 5.26: NMDS ordination (Bray-Curtis dissimilarity) of plot-level vegetation composition (stress = 0.147). Points are coloured by site type (open bog = red, bog forest = green, drained bog = blue) and shaped by drainage-related feature class (open bog plots: open squares with cross; bog forest plots: filled circles; drained bog plots: mounts = plus symbols, former surfaces = filled squares, drainage ditches = filled triangles)

Fitting environmental variables onto the ordination (envfit) showed that water content of the topsoil, degree of peat decomposition, and canopy density were significantly correlated with the observed compositional patterns (Fig. 5.27). The strongest relationships were found for peat decomposition (r^2 = 0.662, p = 0.001) and water content (r^2 = 0.583, p = 0.001), followed by canopy density (r^2 = 0.347, p = 0.001). In contrast, soil pH showed no significant relationship with the ordination configuration (r^2 = 0.075, p = 0.249).

The fitted vectors indicate a pronounced gradient in vegetation composition from plots characterized by high water content, low degrees of peat decomposition and low canopy density towards plots with lower water availability, more advanced peat decomposition and higher canopy cover (Fig. 5.27). Along this gradient, open bog plots were predominantly associated with the wetter and less decomposed end of the ordination space, whereas drained bog plots were mainly positioned towards the drier, more strongly decomposed and more densely shaded part of the gradient.
Within the drained bog, drainage ditch plots were primarily associated with the wetter and less decomposed end of the gradient, while mount plots were located towards the driest and most strongly decomposed part of the ordination space. Former surface plots occupied intermediate positions and partly overlapped with both mounts and drainage ditches. Bog forest plots were located between open bog and drained bog plots, reflecting intermediate site conditions.

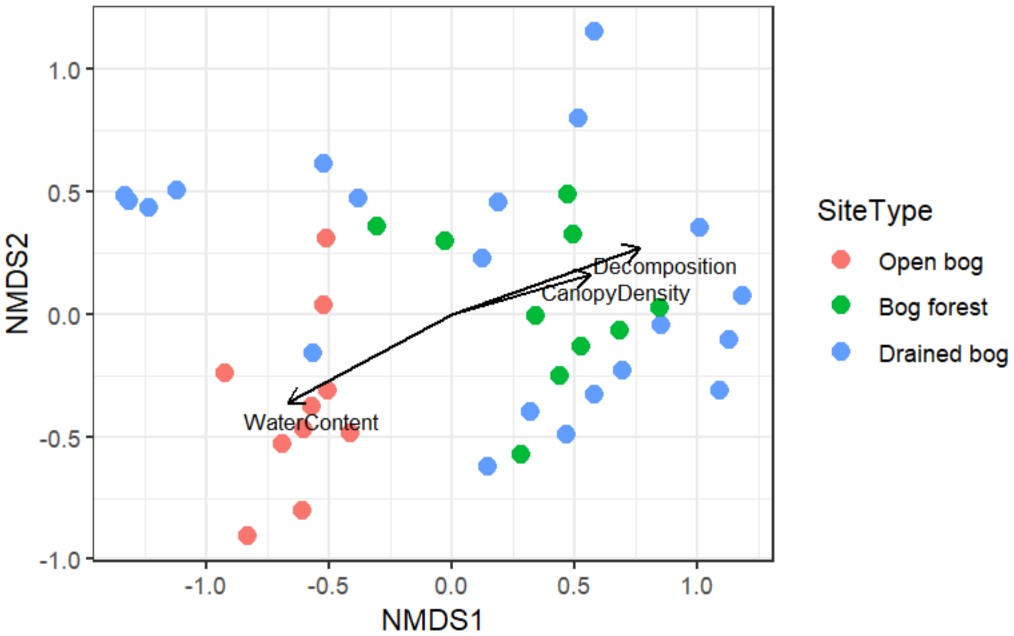

Figure 5.27: NMDS ordination (Bray-Curtis dissimilarity; stress = 0.147) with fitted, significant environmental vectors (envfit; 999 permutations). Points are colored by site type (open bog = red, bog forest = green, drained bog = blue). Arrow length indicates the strength of correlation between each environmental variable and the ordination configuration

5.6. Ecological indicator values and site conditions

5.6.1. Distribution of cover-weighted indicator values across site types and drainage features

To characterize ecological gradients in vegetation composition beyond species identities, cover-weighted mean Landolt indicator values were calculated for each plot and separately for bryophytes and vascular plants (Fig. 5.28 and 5.29). The here considered indicator values describe ecological preferences of species with respect to temperature (T), moisture (F), light availability (L), nutrient availability (N), substrate reaction (R) and humus content (H). Low indicator values correspond to colder, darker, drier, more nutrient-poor and more acidic conditions, whereas higher values indicate warmer, brighter, wetter and more nutrient-rich environments as well as higher humus availability.

Across all site types, moisture indicator values (F) (Fig. 5.28) clearly reflected the hydrological gradient of the study area. For bryophytes, mean moisture values were highest in the open bog (median F ≈ 4.0), indicating permanently moist but not waterlogged substrates (description of indicator values is in Appendix F) and decreased slightly towards the bog forest and the drained bog (median F ≈ 3.5-3.7), corresponding with moist to more mesic conditions. A comparable pattern was observed for vascular plants, with median F values of approximately 3.9 in the open bog, 3.3 in the bog forest and 3.2 in the drained bog, indicating a shift from very moist towards moderately moist site conditions.

Light indicator values (L) showed pronounced differences among site types (Fig. 5.28). For bryophytes, median L values were highest in the open bog (≈ 4.0), corresponding to open, well-lit conditions, and decreased towards the bog forest and drained bog (medians ≈ 3.5-3.6), reflecting a transition towards semi-shaded settings. For vascular plants, this contrast was even more pronounced, with median L values of about 3.4 in the open bog, but only around 2.0-2.2 in the bog forest and drained bog, indicating predominantly to shaded conditions under forest canopies.

Nutrient indicator values (N) were generally low across all site types (Fig. 5.28), confirming the oligotrophic character of the investigated peatland system. Bryophyte communities showed median N values of approximately 2.2 in the open bog and around 1.8-1.9 in the bog forest and drained bog, corresponding to infertile to slightly intermediate substrates, reflecting nutrient poor conditions of the peat substrate. For vascular plants, median N values ranged from about 1.6 in the open bog to approximately 2.4 in the bog forest and drained bog. This indicates, through change from very infertile to infertile substrate towards a slightly medium infertile substrate, a slight increase in nutrient availability in forested and drained areas.

Reaction values (R) were consistently low and showed little variation among site types (Fig. 5.28). Both bryophytes and vascular plants exhibited median R values close to 2, corresponding to acidic to very acidic substrate conditions throughout the study area.

Humus indicator values (H) were, as depicted in Fig. 5.28, uniformly high for both taxonomic groups. Median values were close to 5 for all site types, reflecting the dominance of peat and raw humus substrates typical of raised bog and bog woodland environments.

Temperature indicator values (T) varied only slightly among site types. Median T values for both bryophytes and vascular plants ranged around 2.6-3.0, corresponding to montane to lower subalpine climatic conditions, and therefore mainly reflect the regional climatic setting rather than differences among site types.

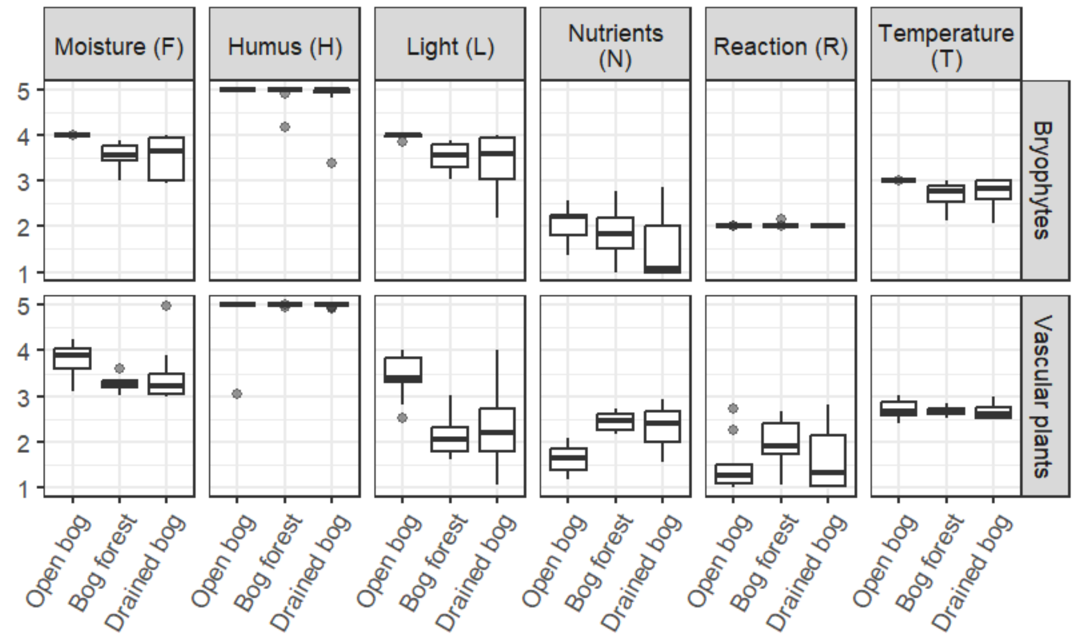

Figure 5.28: Community-weighted mean Landolt indicator values (Temperature T, Moisture F, Light L, Nutrients N, Reaction R and Humus H) of bryophytes and vascular plants for the three investigated site types (open bog, bog forest and drained bog). Indicator values were calculated as cover-weighted means per plot and are shown separately for both taxonomic groups. Boxes represent the interquartile range with median, whiskers indicate 1.5 x IQR and points represent individual plots

Within the drained bog, drainage-related microtopographic features showed a clear differentiation in several indicator values (Fig. 5.29).

Bryophyte moisture values (F) were highest in drainage ditches (median ≈ 4.0), indicating permanently wet or frequently submerged substrates, intermediate on former surfaces (median ≈ 3.8), and lowest on mounts (median ≈ 3.0), reflecting comparatively dry to moderately moist conditions on elevated peat piles. A similar gradient was observed for vascular plants, with median F values increasing from approximately 3.0 on mounts to around 3.2 on former surfaces and 3.9 in drainage ditches.

Light indicator values (L) also varied among features (Fig. 5.29). For bryophytes, median L values increased from mounts (≈ 3.0) to former surfaces (≈ 3.8) and were highest in drainage ditches (≈ 4.0). For vascular plants, mounts were characterized by low median L values (≈ 1.6), reflecting shaded conditions under forest canopies, whereas drainage ditches reached substantially higher values (≈ 3.3), indicating more open light conditions.

Nutrient indicator values (N) remained low for all features (Fig. 5.29) but were lowest for bryophytes on mounts and in drainage ditches (median ≈ 1.0), and slightly higher on former surfaces (median ≈ 2.3). For vascular plants, median N values ranged between approximately 2.0 and 2.6, indicating low to moderately low nutrient availability across all drained-bog features.

Reaction (R) and humus (H) values again showed little variation among features (Fig. 5.29). Median R values remained around 2 for both bryophytes and vascular plants, confirming acidic substrate conditions, while H values were consistently close to 5, indicating peat-dominated, humus-rich substrates.

Temperature values (T) again showed only minor differences among features, with median values between approximately 2.5 and 3.0, corresponding to subalpine to montane climatic conditions.

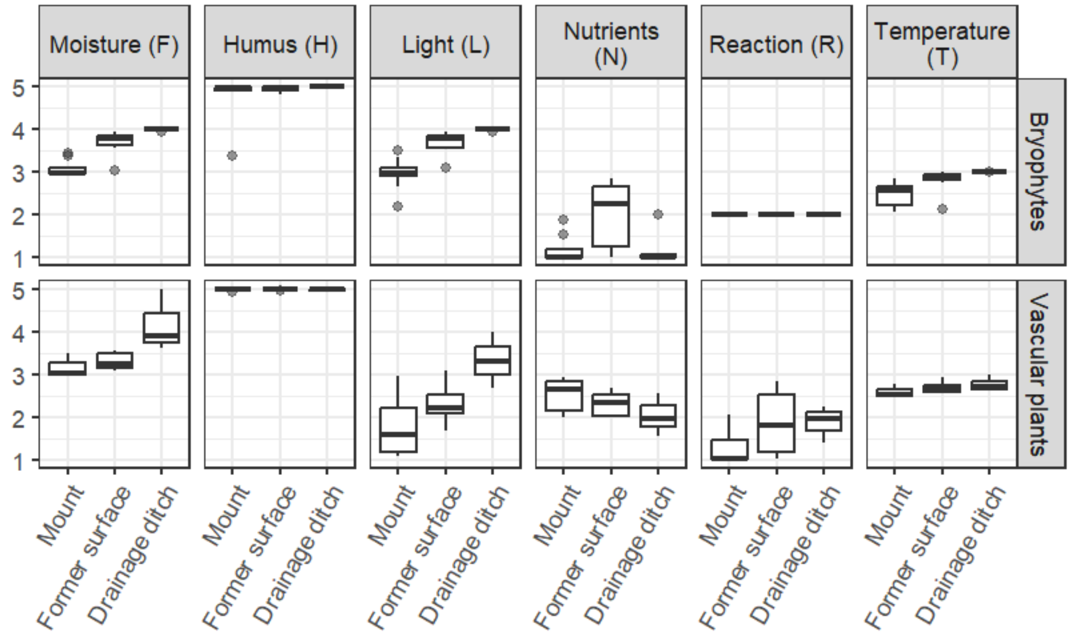

Figure 5.29: Community-weighted mean Landolt indicator values (Temperature T, Moisture F, Light L, Nutrients N, Reaction R and Humus H) of bryophytes and vascular plants for drainage-related features within the drained bog site (mounts, former surfaces and drainage ditches). Indicator values were calculated as cover-weighted means per plot and are shown separately for both taxonomic groups. Boxes represent the interquartile range with median, whiskers indicate 1.5 x IQR and points represent individual plots

5.6.2. Relationship between indicator values and measured environmental variables

To evaluate how well vegetation-based indicator values reflect the measured site conditions, cover-weighted mean Landolt indicator values were correlated with the corresponding environmental variables recorded in the field. Correlations were calculated separately for bryophytes and vascular plants in order to account for the different indicator systems applied to the two taxonomic groups (Fig. 5.30).

The strongest and most consistent relationships were observed for the moisture indicator values (F) in relation to both measured soil water content and peat decomposition (Fig. 5.30).

For bryophytes, moisture indicator values were very strongly and positively correlated with soil water content (Spearman's $\rho = 0.897$, $p_{adj} < 0.001$), and strongly negatively correlated with peat decomposition (Von Post scale; $\rho = -0.798$, $p_{adj} < 0.001$). This indicates that bryophyte assemblages characterized by higher moisture preferences occurred mainly on wetter plots and on weakly decomposed peat.

A similar pattern was found for vascular plants. Moisture indicator values were positively correlated with soil water content ($\rho = 0.627$, $p_{adj} < 0.001$) and negatively correlated with peat decomposition ($\rho = -0.584$, $p_{adj} = 0.002$). Thus, vascular plant communities

indicative of moist to wet conditions were likewise associated with higher water availability and lower degrees of peat decomposition.
According to the Landolt scale, higher F values represent moist to wet substrates (vascular plants: values ≥ 3.5 indicating moist to very moist and ≥ 4.5 wet to flooded sites; bryophytes: values ≥ 4 indicating moist to wet substrates). The observed correlations therefore demonstrate a close correspondence between the indicator values and the measured hydrological gradient within the study area.

Light indicator values (L) were consistently related to canopy density (Fig. 5.30). For bryophytes, L values showed a moderate negative correlation with canopy density ($\rho = -0.456$, $p_{adj} = 0.039$), indicating decreasing light availability with increasing tree cover. This relationship was even more pronounced for vascular plants ($\rho = -0.583$, $p_{adj} = 0.002$). Plots characterized by higher proportions of shade-tolerant species (lower Landolt L values) were associated with higher canopy densities, whereas plots dominated by light-demanding species occurred mainly under more open conditions.
According to the Landolt scale, low L values indicate shade to semi-shade conditions, while higher values represent well-lit to fully open sites. The negative relationships therefore reflect the strong control of forest cover on the light regime across the investigated bog and bog forest habitats.

For vascular plants, nutrient indicator values (N) were positively correlated with peat decomposition ($\rho = 0.618$, $p_{adj} < 0.001$) (Fig. 5.30). This indicates an increasing representation of species associated with higher nutrient availability at sites with more strongly decomposed peat.
In contrast, bryophyte nutrient indicator values showed no significant relationship with peat decomposition ($\rho = -0.160$, $p_{adj} = 1.0$).
This suggests that nutrient-related indicator responses were mainly expressed by vascular plants, whereas bryophyte assemblages were primarily structured by hydrological rather than trophic conditions.

Reaction indicator values (R) showed no significant relationships with measured soil pH for either taxonomic group. For bryophytes, the correlation between R and pH was very weak ($\rho = -0.080$, $p_{adj} = 1.0$), and for vascular plants likewise weak and non-significant ($\rho = -0.179$, $p_{adj} = 1.0$).
Despite the fact that the Landolt reaction values represent species' preferences along an acidity gradient (from strongly acidic to neutral or alkaline substrates), the limited pH range recorded in the study area appears insufficient to produce a clear vegetation-based signal.

Overall, the strongest correspondence between vegetation-based indicator values and measured environmental conditions was observed for moisture and peat decomposition, and for light availability in relation to canopy density (Fig. 5.30).

In contrast, reaction and nutrient indicator values showed weaker or inconsistent relationships with the corresponding measured soil parameters.

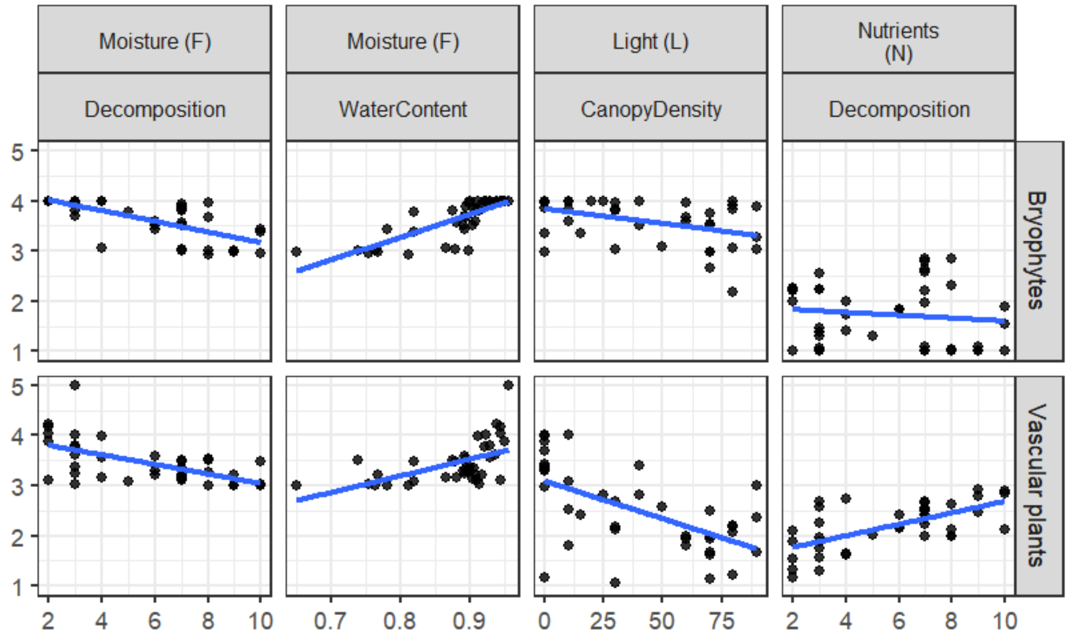

Figure 5.30: Relationships between cover-weighted mean Landolt indicator values and measured environmental variables for bryophytes and vascular plants.
Shown are scatterplots of Landolt moisture (F) versus soil water content and peat decomposition, Landolt light (L) versus canopy density, and Landolt nutrient values (N) versus peat decomposition.
Blue lines represent fitted linear trends for visualization. Each point represents one vegetation plot

6. Discussion

This chapter discusses the effects of long-term drainage and peat decomposition on vegetation composition, structure and site conditions of an alpine upland raised bog system and evaluates the applicability of ecological indicator values for the assessment of restoration-relevant environmental parameters. The results are interpreted in relation to the formulated hypotheses and existing concepts of raised bog degradation and succession. Particular emphasis is placed on shifts from ombrotrophic raised bog communities towards transitional and forest-influenced vegetation, on changes in *Sphagnum* and other bryophyte dominance along hydrological and decomposition gradients, and on the consistency between vegetation-based indicator values and measured site variables.

The discussion is structured according to the individual hypotheses and integrates floristic patterns, multivariate analyses and indicator-based assessments in order to provide an integrated interpretation of vegetation changes after approximately 60 years of drainage.

6.1. Effects of long-term drainage on vegetation composition and structure

This study aimed to assess how long-term drainage and peat decomposition have altered vegetation composition and site conditions in an upland raised bog system in the Austrian alps. The results clearly confirm that the drained site differs significantly in both species composition and vegetation structure from the open raised bog reference site.

Multivariate analyses revealed a clear separation between plots located in the open bog and those of the drained site, indicating a strong shift in species composition along the drainage gradient. Significant differences among site types, as detected by PERMANOVA, further confirm that drainage represents a major driver of vegetation differentiation at the study site. These compositional shifts are accompanied by marked changes in vegetation structure, particularly in the dominance and composition of the bryophyte layer and in the increasing importance of vascular plants and woody species.

In the open bog, vegetation remains largely characterized by continuous carpets and hummocks of peat-forming *Sphagnum* species and by a high constancy of raised bog associated dwarf shrubs and graminoids. In contrast, the drained site is characterized by a heterogeneous vegetation mosaic in which peat-forming *Sphagnum* species are locally reduced or restricted to specific microhabitats, while forest bryophytes including *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum scoparium* become more prominent. At the same time, the cover and frequency of vascular plants associated with drier and more forest-influenced conditions, such as *Vaccinium myrtillus* and *Molinia caerulea*, increase markedly.

Structural changes are further reflected by the higher importance of the shrub and tree layers within the drained site. Regeneration and local dominance of tree species, particularly *Picea abies* and birch species, as well as the frequent occurrence of *Frangula alnus* in the shrub layer, contribute to a more vertically stratified vegetation structure compared to the largely open and *sphagnum*-dominated vegetation of the open bog. These patterns are consistent with the observed increase in canopy density and the associated reduction in light availability along the drainage gradient.
Although some typical raised bog species persist within parts of the drained site, their spatial distribution and dominance patterns differ fundamentally from those in the open bog. Their occurrence is largely confined to locally wetter or less decomposed microsites, such as former bog surfaces or sections close to the open bog margin. This indicates that long-term drainage has not resulted in a complete replacement of raised bog vegetation but instead has produced structurally and floristically altered communities in which remnants of ombrotrophic vegetation persist within a matrix of more advanced successional stages.

Overall, the combined floristic, structural and multivariate evidence demonstrates that long-term drainage has substantially altered both the composition and the physiognomy of the vegetation. The drained site therefore represents a distinctly modified ecosystem compared to the open raised bog. These findings are consistent with the conceptual understanding of drainage-driven vegetation change in raised bogs, where a persistent lowering of the water table disrupts the positive feedbacks maintained by peat-forming *Sphagnum* species and promotes the establishment of forest-related species and alternative vegetation states (Frankl & Schmeidl, 2000; Rydin & Jeglum, 2013).

6.2. Shift towards transitional and forest-related vegetation types

The results further indicate that the vegetation of the drained site shows a substantially higher similarity to forest-influenced and transitional communities than to typical raised bog assemblages. This is reflected by the dominance patterns in the moss and herb layers, the high cover of dwarf shrubs and forest mosses, and the generally higher tree and canopy cover in the drained plots. Although several species typically associated with raised bogs are still present in parts of the drained site, they occur mostly at lower cover and are spatially restricted to wetter microhabitats, particularly along drainage ditches and locally moist former bog surfaces. This indicates that remnants of bog vegetation persist but no longer determine the overall community structure.

The NMDS ordination clearly indicates that, while there are overall differences between the investigated feature types, the vegetation of the drained bog site is floristically more closely related to the bog forest reference site than to the open raised bog. In the ordination, plots from the drained site cluster predominantly in the same region of the ordination space as plots from the bog forest, whereas open bog plots form a clearly separated group. This spatial proximity reflects a pronounced similarity in species composition between drained and forested bog plots. In contrast, open bog plots are characterized by a distinct assemblage dominated by typical raised bog species and are separated along the main compositional gradient. The ordination therefore supports the interpretation that drainage has shifted vegetation composition away from typical open raised bog communities and towards forest-influenced assemblages. This pattern is consistent with the significant overall differences in species composition among site types detected by the PERMANOVA and specifically underlines that the drained bog does not represent an intermediate state between open bog and forest at random but is floristically more similar to the bog forest than to the open raised bog.

The plant community assignment further supports this compositional shift towards forest-influenced vegetation at the drained site. Both the bog forest and the drained bog plots are best assigned to communities of the alliance *Vaccinio-Piceion* within the class *Vaccinio-Piceetea*, which comprises dwarf-shrub-rich spruce and bog woodland communities. In both site types, characteristic species of this syntaxonomic unit, such as *Picea abies*, *Vaccinium myrtillus*, *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum scoparium*, are well represented. The drained bog additionally shows the highest agreement with the association *Bazzanio-Piceetum*, a spruce-dominated mire-margin forest community developing on peat substrates at the transition between raised bogs and mineral soil forests. In contrast, the open bog plots correspond to communities of the class *Oxycocco-Sphagnetea* and the alliance *Sphagnion magellanici*, representing typical open raised bog vegetation. The syntaxonomic differentiation therefore clearly indicates that the drained bog vegetation has undergone a shift from raised-bog communities towards forest-related mire and bog woodland communities, closely resembling the vegetation structure and species composition of the bog forest.

These patterns support the first hypothesis that drained bog areas resemble transition or forest-influenced communities rather than raised bog vegetation. The observed vegetation structure of the drained site is characterized by a more heterogeneous vertical structure, higher shrub and tree cover, and a bryophyte layer dominated by non-peat-forming species, in clear contrast to the largely open, Sphagnum-dominated structure of the open bog.

Comparable shifts towards forest-dominated or transition-mire vegetation after drainage have been reported from boreal and temperate peatlands (e.g. Talbot et al., 2010; Maanavilja et al., 2014; Haapalehto et al., 2017). However, the present study demonstrates that similar long-term successional trajectories also occur in alpine raised bog systems, despite differing climatic conditions. In these studies, drainage associated with forestry management resulted in a marked increase in tree and shrub cover, a decline of peat-forming *Sphagnum* species and a parallel expansion of forest bryophytes and vascular plant species typical of spruce and birch mire forests. This close agreement indicates that the vegetation development observed at the drained site in the present study follows the same hydrologically driven successional pathways that have been described for forestry-drained peatlands.

6.3. Hydrological and peat decomposition gradients and responses of typical intact raised bog species

The second and third hypotheses addressed the response of typical intact raised bog species to hydrological change and peat decomposition, and the contrasting response of peat-forming and non-peat-forming bryophytes.

Typical species of intact raised bogs were defined as *Sphagnum magellanicum*, *S. angustifolium* and *S. capillifolium*, as well as the vascular plant species *Vaccinium oxycoccos*, *Vaccinium uliginosum*, *Eriophorum vaginatum* and *Andromeda polifolia,* following the floristic description of active raised bogs for Austria by Ellmauer and Traxler (2001). These species represent the core floristic elements of ombrotrophic raised bog vegetation and are characteristic of the *Sphagnion magellanici* and intact raised bog habitat types.

Across the investigated site types and drainage-related features, the occurrence of species typical of intact raised bogs shows a clear and structured pattern. The open bog is clearly dominated by typical intact raised bog species, with frequent occurrence of the characteristic vascular plants and a pronounced dominance of peat-forming *Sphagnum* species in the bryophyte layer.
In the bog forest, typical raised bog vascular plants are absent, whereas *Sphagnum* species still contribute a substantial proportion to the bryophyte layer, indicating that ombrotrophic bog elements persist under drier, more decomposed bog forest conditions. A comparable pattern is observed on the former surface features of the drained site, where *Sphagnum* species occur with similarly high cover values, but typical intact raised bog vascular plants are almost completely missing. In contrast, the mount features are characterized by both the absence of typical raised bog vascular plants and generally low cover of *Sphagnum* species. The drainage ditch features, however, are again strongly dominated by *Sphagnum*, and locally also support typical raised bog vascular plants, reflecting the permanently water-saturated conditions prevailing in these microhabitats.

The results clearly demonstrate that both species composition and site conditions vary along a pronounced hydrological and peat decomposition gradient. In the NMDS ordination, water content and peat decomposition were the strongest environmental drivers structuring the vegetation patterns, and both variables showed highly significant relationships with the species composition. Plots characterized by high water content and low peat decomposition clustered closely with the open bog site, whereas plots with lower water content and higher degrees of peat decomposition were associated with the drained bog and, to a lesser extent, with the bog forest.

Along this gradient, a clear decline in the importance of typical intact raised bog species was observed. These species were largely confined to plots with high water content and low peat decomposition, particularly within the open bog site and locally within wet microhabitats of the drained bog, such as drainage ditches and moist former surfaces. In contrast, their occurrence and cover were strongly reduced on drier and more decomposed peat, especially on mounts and within forest-influenced parts of the drained site.

This pattern supports the second hypothesis that both the richness and the cover of typical intact raised bog species decline with decreasing soil water content and increasing peat decomposition. In particular, the vascular bog specialists *Vaccinium oxycoccos*, *Vaccinium uliginosum*, *Eriophorum vaginatum* and *Andromeda polifolia* were largely restricted to the open bog, while they were basically completely absent from strongly decomposed and relatively dry microsites. A congruent observation could be made for the three *Sphagnum* species found, which were partially still present along these environmental gradients but showed clearly different dominances.

The response of bryophytes further confirms the third hypothesis. Along the drainage and decomposition gradient, the cover of peat-forming *Sphagnum* species (*S. magellanicum*, *S. angustifolium* and *S. capillifolium*) decreased markedly, whereas non-peat-forming bryophytes increased in both frequency and cover. This shift was particularly evident in the drained bog site, where forest mosses and disturbance-tolerant bryophytes became dominant on mounts and on former bog surfaces, while *Sphagnum* remained abundant mainly in the permanently wet drainage ditches.
The NMDS ordination and the fitted environmental vectors show that this replacement of peat-forming mosses by non-peat-forming bryophytes closely follows decreasing water availability and increasing peat decomposition. These results indicate that drainage not only alters species composition but also leads to a functional shift in the bryophyte layer, from peat-forming communities towards forest- and disturbance-associated moss assemblages.

The observed decline of peat-forming *Sphagnum* species and the parallel increase of non-peat-forming bryophytes and vascular plants along the drainage and decomposition gradient is consistent with patterns reported from long-term drainage studies in boreal and temperate raised bogs. Several studies have demonstrated that even moderate and persistent lowering of the water table disrupts the positive feedback between *Sphagnum* growth and near-surface water saturation, thereby promoting alternative vegetation states dominated by forest and transitional mire species (Frankl & Schmeidl, 2000; Rydin & Jeglum, 2013). Comparable shifts from *Sphagnum*-dominated communities towards bryophyte and vascular plant assemblages typical of drained or forest-influenced peatlands have been documented in boreal raised bogs and spruce swamp forests following drainage (Talbot et al., 2010; Maanavilja et al., 2014). In these systems, *Sphagnum* cover commonly declines while feather mosses and other non-peat-forming bryophytes increase, particularly on drier and more decomposed peat surfaces. Similar patterns were also reported for long-term drained temperate peatlands, where bog specialist species were gradually replaced by forest and shrub-dominated vegetation (Pinceloup et al., 2020; Haapalehto et al., 2017).

Although the present study covers a much smaller spatial extent and a single alpine bog complex, the strong alignment of vegetation changes with water content and peat decomposition indicates that the same hydrologically mediated vegetation shifts operate in the Krumauer Moor.

6.4. Applicability of Landolt indicator values for assessing site conditions

This section evaluates whether Landolt indicator values derived from the vegetation can be used as proxies for site conditions relevant for peatland revitalization. The assessment is based on the relationships between community-weighted mean Landolt values and measured environmental variables presented in Section 5.5.

Beyond the statistical correlation analyses, the general magnitude of the cover-weighted Landolt indicator values corresponded well to the measured site conditions. Across all plots, gravimetric soil water content was consistently high (around 80-90 %), which is reflected in predominantly moist to moderately moist moisture indicator values. Similarly, measured pH values and decomposition levels were in agreement with the generally low reaction and nutrient indicator values typical for raised bog systems. This overall correspondence suggests that, despite limitations in plot-scale precision, Landolt indicator values adequately capture the general ecological character of the investigated peatland sites.

Because Landolt indicator values are defined separately for vascular plants and bryophytes, both taxonomic groups were analyzed independently. Nevertheless, the following discussion is structured along the investigated environmental gradients, as the ecological interpretation of the results is comparable for both groups.

The strongest and most consistent relationships were found for moisture-related gradients.

Community-weighted Landolt moisture values (F) showed a very strong positive correlation with measured water content and a strong negative correlation with peat decomposition for both bryophytes and vascular plants.

This indicates that vegetation-based moisture values reliably reflect both present hydrological conditions and longer-term drainage effects expressed by increasing peat decomposition. The close correspondence between Landolt F and these two hydrological indicators confirms that the vegetation integrates site conditions over longer time periods and is therefore well suited to represent persistent drainage impacts rather than short-term surface moisture only.

This result is fully consistent with the general conceptual understanding of ecological indicator values. Schaffers and Sýkora (2000) emphasized that indicator values reflect the realized ecological niche of species and thus integrate long-term environmental conditions. Diekmann (2003) similarly highlighted that Ellenberg- and Landolt-type moisture indicators perform particularly well along broad hydrological gradients and are among the most robust indicator dimensions.
Recent syntheses further confirm that moisture values are generally the most reliable proxies among indicator systems and show the strongest correspondence with independently measured environmental data, including in wetland and peatland contexts (Ivanova & Zolotova, 2023).
In the present study, the strong relationships between Landolt F, soil water content and peat decomposition therefore demonstrate that vegetation-based indicator values can reliably characterize drainage gradients that are directly relevant for restoration planning.

Landolt light values (L) showed a clear and significant negative relationship with canopy density for both bryophytes and vascular plants. Plots characterized by dense tree cover exhibited consistently lower light indicator values, whereas open bog and open drainage features showed higher values.
This pattern confirms that Landolt L accurately reflects the light regime of the ground and field layers and closely tracks structural changes associated with forest encroachment. Similar results have been reported in calibration studies of indicator values, where light values were found to correspond well with measured or modelled light availability, especially in forest and transitional ecosystems with strong gradients (Diekmann, 2003; Ivanova & Zolotova, 2023).
In the context of drained peatlands, this relationship can be of relevance because canopy development represents one of the most pronounced structural consequences of long-term drainage. The present results therefore demonstrate that Landolt light values provide an effective vegetation-based proxy for shading and forest influence.

In contrast to moisture and light, the performance of nutrient-related indicator values was more differentiated.
For vascular plants, Landolt nutrient values (N) showed a significant positive relationship with peat decomposition. Increasing nutrient indicator values with increasing decomposition indicate a shift towards species associated with more nutrient-enriched and biologically active peat conditions. This is ecologically plausible, as peat decomposition reflects increasing aeration, enhanced microbial activity and altered nutrient cycling.
For bryophytes, however, the relationship between Landolt N and peat decomposition was weak and not statistically significant. This difference between taxonomic groups likely reflects the distinct ecological strategies of bryophytes, such as the absence of roots, which might therefore be more strongly controlled by moisture and microhabitat conditions than by nutrient availability in the substrate.

Such taxon-specific responses are well documented in the literature. Diekmann (2003) emphasized that the interpretability of nutrient indicator values is more context dependent and may vary among vegetation layers and functional groups. Ivanova and Zolotova (2023) similarly concluded that nutrient-related indicator values generally show higher uncertainty and are more sensitive to community composition and regional species pools than moisture or light indicators.
Overall, the present results suggest that Landolt nutrient values may capture broader productivity and decomposition-related gradients in vascular plant communities but are less suitable for describing nutrient conditions based on bryophyte assemblages.

No significant relationship was detected between Landolt reaction values (R) and measured soil pH in the upper layer for either bryophytes or vascular plants.
While the indicator values generally point towards acidic substrate conditions, this weak correspondence is most likely explained by the very narrow and uniformly acidic pH range across all investigated plots. Under such conditions, even ecologically meaningful variation in species composition cannot be expected to translate into strong statistical relationships with measured pH.
This limitation is well recognized in indicator value research. Schaffers and Sýkora (2000) and Diekmann (2003) both stressed that indicator values describe realized niche optima along ecological gradients and that their performance strongly depends on the extent of the underlying environmental gradient. When gradients are short or truncated, relationships between indicator values and measured variables are inevitably weak.
In addition, Ivanova and Zolotova (2023) highlighted that reaction and nutrient indicator values are generally less reliable for quantitative estimation of chemical soil properties and should primarily be interpreted as qualitative descriptors of site conditions.

Although separate indicator systems were applied for bryophytes and vascular plants, both groups exhibited highly consistent responses along the main hydrological and structural gradients. In both cases, moisture and light values showed strong and ecologically coherent relationships with measured variables, whereas chemical parameters were only weakly reflected.
This convergence indicates that hydrology and canopy structure represent the dominant drivers of vegetation differentiation in the study area and supports the robustness of the detected gradients.

It is important to highlight that ecological indicator values do not represent direct measurements of environmental parameters. Instead, they describe the realized ecological niche of species and therefore integrate multiple environmental influences, competitive interactions and historical site conditions.
Consequently, even strong correlations cannot be interpreted as direct quantitative relationships between indicator values and physical variables such as soil water content or peat decomposition. As discussed by Schaffers and Sýkora (2000) and Diekmann (2003), indicator values may deviate from physiological optima and are influenced by

species turnover and community context. Ivanova and Zolotova (2023) further emphasized that the transferability of indicator values is constrained by biogeographical and vegetation-type specific conditions.

This conceptual difference between vegetation-based proxies and directly measured variables represents an inherent limitation of the approach and must be considered when applying Landolt values for restoration-oriented site assessment.

6.5. Indicator species and the limitations of single-taxon interpretation

The distribution of species that are traditionally regarded as indicators of intact or disturbed raised bog conditions illustrates the limitations of a single-taxon approach for assessing site status in long-drained and structurally heterogeneous peatlands.

In the open bog, vegetation was clearly dominated by species typical of intact raised bogs, including *Sphagnum magellanicum*, *S. angustifolium* and *S. capillifolium* in the moss layer and the vascular plants *Vaccinium oxycoccos*, *Vaccinium uliginosum*, *Eriophorum vaginatum* and *Andromeda polifolia*, which occurred with high frequency and, partly, high cover. At the same time, several species commonly interpreted as disturbance or drying indicators, such as *Molinia caerulea*, *Calluna vulgaris* and *Vaccinium myrtillus*, were also frequent and locally reached moderate cover values. The co-occurrence of these contrasting indicator groups demonstrates that even the reference open bog site cannot be interpreted as an undisturbed system solely based on the presence of characteristic bog species.

In the bog forest, typical vascular plant species of intact raised bogs were entirely absent. Nevertheless, species that are often treated as disturbance indicators in open bog contexts but are also characteristic of bog-influenced forest communities (e.g. *Molinia caerulea*, *Vaccinium myrtillus*, *Picea abies* and *Betula* spp.), were widespread and formed a substantial part of the vegetation. In contrast to the absence of typical vascular bog specialists, peat-forming *Sphagnum* species were still consistently present and contributed markedly to the ground layer. This combination reflects the transitional character of bog woodland vegetation, in which forest species and bog specialists coexist under modified but still oligotrophic and wet conditions.

Within the drained bog site, the distribution of typical intact raised bog species was strongly feature-dependent. In the drainage ditches, several typical bog species, particularly *Sphagnum* species and locally also *Eriophorum vaginatum*, occurred, reflecting permanently water-saturated microsites. On the former surfaces, *Sphagnum* species were still present with notable cover, whereas typical vascular bog specialists were almost entirely absent. Instead, species that are frequently regarded as disturbance indicators but remain closely associated with bog and bog-forest environments, such as *Molinia caerulea* and *Vaccinium myrtillus* dominated the vegetation. On the mount features, both typical intact bog species and bog-associated disturbance indicators were absent or significantly less prominent, and vegetation was rather characterized by forest and dry-site bryophytes and vascular plants.

From an ecological perspective, this pattern is consistent with the concept that drainage-driven vegetation change in raised bogs is primarily controlled by hydrological alteration and microtopographic variability, rather than by discrete and uniform successional stages (Frankl & Schmeidl, 2000; Rydin & Jeglum, 2013).

Importantly, the frequent and locally abundant occurrence of species commonly interpreted as indicators of degradation or successional change in the open bog site indicates that this site cannot be considered an intact raised bog. Although several typical intact raised bog species were still widespread and dominant in the moss layer, the consistent presence and in some cases high cover of disturbance-associated species suggest that the open bog represents a hydrologically altered and transitional state rather than a fully functional, undisturbed raised bog system. While some of these species may occur in small patches within natural raised bogs, their high frequency and spatial relevance in the present study point to a long-term modification of site conditions (Eigner, 2003).

Overall, species traditionally used as indicators of either intact raised bogs or degraded conditions showed a strong spatial overlap among site types and microtopographic features. Several typical bog species persisted locally under drained conditions, particularly where small-scale hydrological refugia existed, while species commonly interpreted as disturbance indicators occurred even within the open bog. These patterns are best explained by the long drainage history of the study area, fine-scale hydrological heterogeneity and the persistence of some bog species once established. As a consequence, individual species cannot be interpreted as clear indicators of site condition in this system.

This study therefore supports an integrative interpretation of vegetation patterns. Meaningful ecological assessment of drained and transitional peatlands requires the combined consideration of species composition, relative cover, vegetation structure and environmental gradients, rather than relying on the presence or absence of single indicator taxa.

6.6. Implications for restoration and site assessment

The results of this study provide site-specific indications for the assessment of degradation status and restoration priorities in drained alpine upland raised bog systems. However, the following implications should be interpreted with caution, as environmental parameters were measured only once per plot and therefore represent snapshots rather than long-term site conditions.

Across the investigated plots, hydrological conditions emerged as the primary structuring factor of vegetation patterns. Both the ordination analyses and the correlations between vegetation-based indicators and measured environmental variables consistently indicated that differences in near-surface wetness were closely associated with changes in species composition and vegetation structure. This is in line with the well-established conceptual understanding that vegetation change in raised bogs is fundamentally driven by hydrological alteration, and that drainage disrupts the positive feedback between high water tables and peat-forming *Sphagnum* communities (Frankl & Schmeidl, 2000; Rydin & Jeglum, 2013).

It is important to note that peat decomposition and vegetation change should not be interpreted as independent drivers in this context. Increased peat aeration and decomposition are themselves a consequence of lowered water tables and prolonged drying of the acrotelm. The observed relationships between vegetation patterns, peat decomposition and water content therefore most likely reflect different stages along a common hydrological degradation gradient.

The strong relationship between measured water content and vegetation-based moisture indicator values suggests that plant communities integrate longer-term hydrological conditions more consistently than single field measurements. Similar conclusions have been drawn for the use of Ellenberg and Landolt indicator values as integrative proxies for site moisture in vegetation studies (Diekmann, 2003; Schaffers & Sýkora, 2000; Ivanova & Zolotova, 2023). In this respect, the present results support the applicability of vegetation-based indicators for rapid, plot-scale assessments of hydrological conditions relevant to restoration planning, particularly in systems where continuous hydrological monitoring is not available.

Peat-forming *Sphagnum* species represent a key functional component for restoration assessment. Their high cover and frequency in the open bog site and in permanently wet drainage ditches, contrasted with their strongly reduced occurrence on mounts and, to a lesser extent, on former bog surfaces, indicate a clear sensitivity to drainage-related drying. This pattern is consistent with the widely documented decline of peat-forming *Sphagnum* following water-table drawdown and their central role in maintaining ombrotrophic conditions and peat accumulation (Rydin & Jeglum, 2013). Consequently, the presence and relative dominance of *Sphagnum* species can be considered an important indicator of remaining ecological functioning and potential for hydrological restoration.

In contrast, the increasing dominance of non-peat-forming bryophytes and forest mosses, together with graminoids and dwarf shrubs associated with later successional stages, reflects progressive drying and increasing peat aeration. Comparable shifts from *Sphagnum*-dominated communities towards forest and heath vegetation have been reported for drained and degraded raised bogs in other regions (Eigner, 2003; Talbot et al., 2010; Rydin & Jeglum, 2013). In the present study, the dominance of these species on mounts and across large parts of the drained bog site therefore indicates advanced degradation stages and a reduced short-term restoration potential in the absence of substantial hydrological intervention.

Canopy density further represents an important structural component influencing site conditions. The observed relationship between light indicator values and canopy density suggests that tree and shrub encroachment modifies microclimatic conditions and reinforces successional trajectories towards bog woodland. Similar feedbacks between shading, reduced *Sphagnum* performance and increasing dominance of forest-related species are described for drained bog and bog-forest transition systems (Rydin & Jeglum, 2013). Nevertheless, the present results also indicate that reduced light availability alone cannot explain the observed vegetation patterns, and that canopy effects are closely linked to the underlying hydrological degradation gradient.

The analyses further demonstrate that Landolt indicator values can provide useful complementary information for restoration-relevant site assessment. In particular, moisture and light indicator values showed consistent relationships with measured water content, peat decomposition and canopy density. This supports previous findings that vegetation-based indicator values are especially suitable for representing hydrological and structural site gradients (Diekmann, 2003; Schaffers & Sýkora, 2000; Ivanova & Zolotova, 2023). In contrast, nutrient and reaction indicator values proved to be of limited use for assessing chemical site conditions in the present study. Soil pH showed only minor variation across the study area and did not display a consistent relationship with vegetation-based reaction values. This result is in line with previous studies emphasizing that indicator values for chemical parameters are less reliable when environmental gradients are narrow or when soil measurements represent short-term conditions (Schaffers & Sýkora, 2000; Diekmann, 2003).

Overall, the present results suggest that restoration planning in the Krumauer Moor should primarily focus on restoring high and stable water tables and limiting further drainage effects, as hydrological conditions represent the fundamental control on both peat decomposition and vegetation development. Vegetation-based indicators, especially the abundance of peat-forming *Sphagnum* species, the occurrence of forest mosses and the Landolt moisture and light values, may provide a practical and integrative tool for identifying degradation stages and restoration priorities. At the same time, the applicability of these indicators should be interpreted cautiously and preferably combined with repeated hydrological and soil measurements to better capture long-term site dynamics.

6.7. Limitations of the study

Several methodological and design-related limitations need to be considered when interpreting the results of this study.

First, all environmental variables were recorded as single measurements per plot. Soil water content, peat decomposition (Von Post scale) and soil pH therefore represent only a snapshot of local site conditions. Especially in peatland systems, near-surface hydrological conditions can vary substantially over short time scales in response to weather conditions and seasonal dynamics. Consequently, the measured values cannot be interpreted as long-term hydrological or chemical means, but rather as indicative field-based estimates of relative site conditions.

Second, the vegetation data were collected using small plot sizes (1 x 1 m). While this plot size is well suited to capture fine-scale vegetation patterns and microtopographic variation in bog systems, this approach might limit the representation of spatial heterogeneity at the scale of whole site types and drainage features. In particular, tree and shrub cover as well as transitional vegetation patterns at plot margins may be underrepresented.

Third, the study design focused on a targeted selection of site types and drainage-related microfeatures (open bog, bog forest, drained bog with mounts, former surfaces and drainage ditches). The investigated plots therefore do not represent independent replicates of different peatland systems but rather subsamples within a single bog complex. As a consequence, the results primarily describe spatial patterns within the Krumauer Moor and cannot be directly generalized to other raised bogs without caution.

Fourth, vegetation was recorded during two sampling campaigns within one year (May and August). Although seasonal effects were found to be negligible with respect to species composition and species richness, interannual variability and longer-term vegetation dynamics could not be assessed within the framework of this study.

Finally, several environmental parameters that are ecologically relevant for peatland vegetation, such as nutrient availability and redox conditions, were not measured directly. In addition, peat decomposition was assessed using a field-based Von Post classification, which provides a useful comparative indicator of peat condition but does not replace quantitative laboratory analyses.

Despite these limitations, the combined use of detailed vegetation data, microfeature-based sampling and multiple complementary environmental descriptors allows a robust assessment of relative hydrological and degradation gradients within the study area and provides a sound basis for interpreting vegetation patterns in relation to long-term drainage effects.

7. Conclusion

This study addressed the question of how long-term drainage and associated peat decomposition have altered vegetation composition and site conditions in a raised bog of an inner-alpine valley, and to what extent ecological indicator values can be used to estimate site conditions relevant for revitalization. By comparing a drained bog site with open bog and bog forest, and by explicitly considering microfeatures within the drained area, the results provide a differentiated picture of vegetation change after approximately six decades of drainage at Krumauer Moor.

The analyses clearly demonstrate that vegetation composition differs significantly among the investigated site types. Ordination and permutation-based tests consistently separated open bog, bog forest and drained bog plots, confirming that long-term drainage and canopy development have led to pronounced and persistent shifts in plant communities. In line with the initial expectations, plots from the drained bog were floristically more similar to bog forest than to open bog vegetation, and both site types are characterized by species assemblages and dominance patterns typical of forest-related mire communities, resulting in the assignment to the same plant community, the *Bazzanio-Piceetum*. In contrast, open bog plots form a clearly distinct assemblage dominated by ombrotrophic raised bog species. The here investigated drained bog therefore does not represent a random or intermediate vegetation state but reflects a directional shift away from open raised bog communities towards forest-influenced assemblages.

Environmental gradients, particularly soil water content, peat decomposition and canopy density, were strongly associated with vegetation patterns across all site types. These gradients therefore represent the main drivers of the observed community differentiation. Further the responses of typical intact raised bog species and the contrasting behavior of peat-forming and non-peat-forming bryophytes along hydrological and decomposition gradients were confirmed. Typical raised bog species, including peat-forming *Sphagnum* species and characteristic vascular plants, are largely restricted to plots with high water availability and low peat decomposition. Their cover and frequency decline markedly with decreasing soil moisture and increasing peat decomposition.

Within the drained bog, pronounced differences among microfeatures emphasize that drainage effects are spatially heterogeneous. Former surfaces retained relevant *Sphagnum* cover but were almost entirely devoid of typical raised bog vascular plants. Mounts represented the most degraded microhabitats, showing very low *Sphagnum* cover and a complete absence of characteristic raised bog species. In contrast, drainage ditches were strongly dominated by *Sphagnum* and still hosted some typical raised bog vascular plants. These patterns highlight that microtopography and local hydrological conditions strongly mediate vegetation responses to long-term drainage. The observed increase of forest mosses with increasing drainage effects and canopy influence, accompanied by a decline of peat-forming *Sphagnum* species, reflects a shift from peat-accumulating communities towards vegetation types with limited peat-forming capacity.

In contrast to compositional and structural changes, overall species richness does not differ significantly among the main site types. However, richness varies among drainage-related microfeatures, and bryophytes and vascular plants show different richness patterns, despite following similar environmental gradients. These findings underline that changes in community composition and functional structure are more informative indicators of site condition than simple richness metrics. In particular, the replacement of peat-forming bryophytes by forest mosses and the loss of characteristic raised bog vascular plants represent key ecological changes relevant for restoration planning.

The analysis of Landolt indicator values provides an explicit link between vegetation patterns and the assessment of site conditions. Moisture indicator values showed very strong and consistent relationships with measured soil water content and peat decomposition, and light indicator values were strongly related to canopy density. These results support the hypothesis that indicator values can serve as reliable proxies for hydrological and shading conditions in drained alpine raised bogs. In contrast, the performance of chemical indicator dimensions is limited. Nutrient indicator values show only a weak and partly taxon-specific relationship with peat decomposition, and reaction values do not correspond to measured soil pH. This indicates that indicator values might not be suitable for quantitative assessment of chemical site conditions in this system, particularly where environmental gradients are narrow and direct nutrient measurements are lacking. Bryophytes and vascular plants must therefore be treated as separate indicator systems, although both exhibit highly consistent directional responses along the dominant hydrological and structural gradients.

The occurrence of indicator species across different site types further emphasizes that single species cannot be used as reliable surrogates for site condition or restoration status. Disturbance-associated species were also frequent in open bog plots, demonstrating that the site cannot be interpreted as an undisturbed, intact raised bog. Correspondingly, some typical raised bog species persisted within drained areas, especially in drainage ditches. These findings demonstrate that vegetation structure, dominance patterns and community composition must be considered jointly when evaluating degradation and restoration potential. The persistence of *Sphagnum*-dominated vegetation and characteristic vascular plants in selected microhabitats suggests that, even after long-term drainage, parts of the bog still retain ecological properties that may be relevant for revitalization measures, particularly where local hydrological conditions remain favorable.

Overall, the results directly address the research question by showing that long-term drainage and associated peat decomposition have led to a marked shift from open raised bog vegetation towards forest-influenced and structurally altered communities, with strong spatial variability driven by microtopography. Hydrological alteration represents the fundamental driver of this change, while peat decomposition and canopy development reflect different expressions of the same underlying degradation gradient. At the same time, the study demonstrates that vegetation-based indicator values, especially for moisture and light, provide a robust and integrative tool for characterizing restoration-relevant site conditions, whereas in this case chemical site properties could not be reliably correlated with indicator values.

Nonetheless several limitations must be considered when interpreting these findings. All environmental variables were measured only once and thus represent snapshots rather than long-term averages. The chosen plot size may have limited the detection of fine-scale spatial variability, and the study was restricted to a single bog complex, which constrains the generality of the conclusions. Peat decomposition was assessed using the field-based Von Post scale, and no direct measurements of nutrient availability were available. These constraints may have contributed to the weak relationships observed between indicator values and chemical site properties.

Despite these limitations, the consistent separation of site types, the strong relationships between vegetation composition and key environmental gradients, and the coherent responses of both bryophyte and vascular plant communities provide a solid basis for assessing drainage impacts in alpine raised bogs. For peatland restoration and site assessment, the results highlight the importance of explicitly considering microhabitat variability and vegetation structure, rather than relying solely on the presence of individual species or overall species richness. In particular, the strong diagnostic value of moisture and light indicator values supports their application as complementary tools for identifying hydrologically and structurally suitable areas for restoration measures. At the same time, the limited ability of indicator values to reflect chemical conditions underlines the need for direct environmental measurements when evaluating restoration success and long-term ecosystem recovery.

Table of figures

Table of tables

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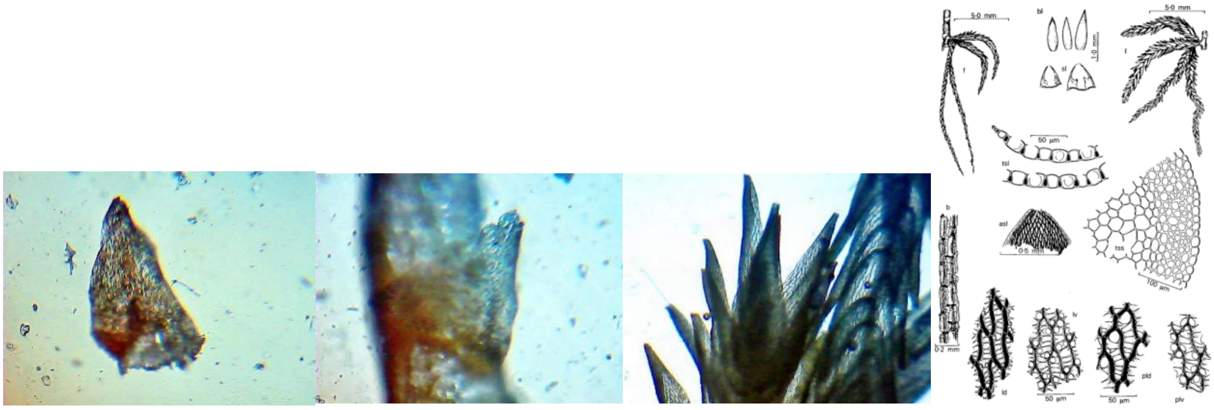
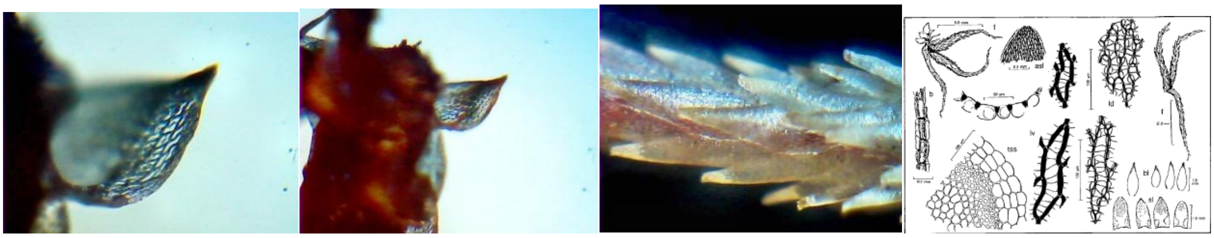
Appendix

A) Microscope photos of *Sphagnum* species



Reference for *Sphagnum angustifolium* identification: (from left to right) single stem leaf; attached stem leaf; tip of a branch with branch leaves and graphic with diagnostic features from Daniels et al. (1985)



Reference for *Sphagnum capillifolium* identification: (from left to right) single stem leaf; attached stem leaf; branch with branch leaves and graphic with diagnostic features from Daniels et al. (1985)

Reference for *Sphagnum magellanicum* identification: (from left to right) single stem leaf; branch leaf and part of a stem; and graphic with diagnostic features from Smith & Smith (2004)

B) Standardized vegetation recording sheet

Examination area: Plot Nr.:	Terrain:	Date; time:	Weather:
Coordinates:	Description/Notes: Canopy cover [%]:		Peat decomposition scale (Von Post):
ID:	Plant species:	abundance-dominance scale (Braun-Blanquet):	Veg. layer [Tree; Shrub; Herb; Moss]:
1			
2			
3			

C) Recorded plot information

Plot Nr.:	Site:	Coordinates:	Terrain:	Description:	Canopy density:
B1	Open bog	47.58330346 14.50134733	Mostly flat; slight hummocks and lawns (ca. 15cm)	Open bog; moist-wet, no surface water	0%
B2	Open bog	47.58376969 14.50092486	Completely flat	Open bog; moist-wet; no surface water; gras dominates herb layer	0%
B3	Open bog	47.58378968 14.50117720	Mostly flat; slight hummocks and lawns (ca. 15cm)	Open bog; moist-wet, no surface water; under some low density trees (mostly dead)	10%
B4	Open bog	47.58352845 14.50119626	Completely flat	Open bog; moist, no surface water; dominated by Calluna, not fully sphagnum covered	0%
B5	Open bog	47.58353441 14.50149601	Not flat, strong hummocks and lawns (25cm)	Open bog; moist-wet, no surface water; Moss mounts next to fallen tree ditch	0%
B6	Open bog	47.58355107 14.50098082	Nearly flat, slight hummocks and lawns (10cm)	Open bog; moist-wet, no surface water; Under some low density trees	25%
B7	Open bog	47.58303638 14.50091823	Slightly tilted north (P.mugo patch), slight hummocks and lawns (10cm)	Semi-open bog; wet, no surface water; Partially covered by P. mugo	40%
B8	Open bog	47.58343990 14.50144950	mostly flat, slightly elevated from surrounding, hummock covers 30%	Open bog; moist-wet, no surface water; Elevated spot	0%
B9	Open bog	47.58351432 14.50135487	not flat, bigger hummock (30cm)	Open bog; moist-wet, no surface water; Mount covered witch V. oxycoccos	0%
B10	Open bog	47.58343715 14.50115021	mostly flat, very slight hummocks and lawns	Open bog; wet-moist, no surface water; Next to fallen P. abies	0%
T1	Bog forest	47.58332373 14.50174142	Mostly flat; one small mount (30cm)	forest >90% cover, moist, strong herb layer	90%
T2	Bog forest	47.58318191 14.50154904	some small mounts (20cm)	forest >80% cover, moist, strong herb + shrub layer	80%
T3	Bog forest	47.58307230 14.50156069	mostly flat	forest <20% cover, wet-moist, weak to medium shrub + herb layer	15%
T4	Bog forest	47.58308180 14.50142903	not flat, multiple mounts (up to 30cm)	forest >60% cover, on animal path, moist-wet, strong herb-no shrub layer	60%
T5	Bog forest	47.58322625 14.50163693	two small mounts (30cm)	forest >90% cover, moist-wet, medium herb + weak shrub layer, next to big P. abies	90%
T6	Bog forest	47.58433636 14.50112905	Mostly flat; one mount crossing (20cm)	forest >70% cover, moist, medium herb - no shrub layer	70%
T7	Bog forest	47.58416763 14.50068566	completely flat	forest >90% cover, moist, medium herb + shrub layer	90%
T8	Bog forest	47.58422686 14.50099537	tree stump mount (30cm)	forest edge <10% cover, moist-wet, medium herb - no shrub layer	10%
T9	Bog forest	47.58391551 14.50023045	mostly flat; some Bulten and Schlenken (20cm)	open forest >60% cover, moist, strong herb - medium shrub layer	60%
T10	Bog forest	47.58423080 14.50079180	mostly flat	forest >80% cover, moist, weak herb - no shrub layer	80%
M1	Drained Bog - Mount	47.5843361 14.5021444	Top of mount; mostly flat	Thick underwood, forest <30% cover, dry-moist, weak herb - strong shrub layer (young trees <2m)	30%
M2	Drained Bog - Mount	47.5840778 14.50198611	Top of mount; tilted south (10-15°)	open forest - no cover, dry, weak herb - strong shrub layer (young trees)	0%
M3	Drained Bog - Mount	47.5840333 14.501875	Top of mount; slightly tilted west, some small mounts	forest >70% cover, dry-moist, medium herb - weak shrub layer	70%
M4	Drained Bog - Mount	47.5834194 14.50197777	Top of mount; next to Bulte; slightly tilted east	open forest - no cover, dry to moist, strong herb - weak to medium shrub layer	0%
M5	Drained Bog - Mount	47.5835972 14.50223055	Top of mount; deep Schlenke (30cm) on the edge; not flat	forest >80% cover, dry-moist, medium herb - weak to no shrub layer	80%
M6	Drained Bog - Mount	47.5836722 14.50181944	Top of mount; nearly flat	slight understory, forest >70% cover, dry to moist, weak herb and shrub layer	70%
M7	Drained Bog - Mount	47.5836111 14.501775	Top of mount; multiple small mounts (20cm)	(open) forest >70% cover, dry-moist, strong herb - no shrub layer	70%
M8	Drained Bog - Mount	47.584225 14.501525	Top of mount; mostly flat	open forest <40% cover, young trees (<4m), moist, strong herb and shrub layer	40%
F1	Drained Bog - Former bog surface	47.5834722 14.50188055	former bog surface; flat	Forest >60% cover, moist, weak to medium herb and weak shrub layer	60%
F2	Drained Bog - Former bog surface	47.5836861 14.50168888	former bog surface; flat	open forest <30% cover, dry-moist, strong to medium herb - no shrub layer	30%
F3	Drained Bog - Former bog surface	47.5841111 14.50149444	former bog surface; small single overgrown tree stump mount (15cm)	open forest <30% cover, moist, medium herb - weak to no shrub layer	30%
F4	Drained Bog - Former bog surface	47.5840222 14.50171666	former bog surface; slight mounts form M. caerulea	open forest <50% cover, dry-moist, strong herb - weak to no shrub layer	50%
F5	Drained Bog - Former bog surface	47.5841361 14.50195277	former bog surface; flat	Forest >70% cover, dry-moist, weak to medium herb and weak shrub layer	70%
F6	Drained Bog - Former bog surface	47.5841917 14.5021166	former bog surface; very slight mounts and narrows	open forest here <10% cover, moist, strong herb - medium shrub layer	10%
F7	Drained Bog - Former bog surface	47.5837667 14.50201666	former bog surface; nearly flat	forest >80% cover, moist-dry, strong to medium herb - no shrub layer	80%
F8	Drained Bog - Former bog surface	47.5835583 14.50218611	former bog surface; flat	Forest 70% cover, dry-moist, weak herb - no to weak shrub layer	70%
D1	Drained Bog - Drainage ditch	47.5836472 14.50208055	Ditch bottom; flat	Forest >80% cover, standing water ~40cm deep (under Sphagnum layer)	80%
D2	Drained Bog - Drainage ditch	47.5839722 14.5014611	Ditch bottom; flat	open forest <10% cover, standing water ~15cm deep (under Sphagnum layer)	10%
D3	Drained Bog - Drainage ditch	47.5840639 14.50135833	Ditch bottom; flat	no forest, standing water ~30cm deep (under Sphagnum layer)	0%
D4	Drained Bog - Drainage ditch	47.5843167 14.50194722	Ditch bottom; flat	open forest <20% cover, standing water ~30cm deep (under Sphagnum layer)	20%
D5	Drained Bog - Drainage ditch	47.5840139 14.5019944	Ditch bottom with edges	Forest >30% cover, standing water ~20cm deep (under Sphagnum layer), ID4-13 growing on steep ditch walls	30%

D) Vegetation survey data

Coverage rates of species [%] of survey in May

Species / Plot + Site	Vegetation layer	B1 Open bog	B2 Open bog	B3 Open bog	B4 Open bog	B5 Open bog	B6 Open bog	B7 Open bog	B8 Open bog	B9 Open bog	B10 Open bog	T1 Bog forest	T2 Bog forest	T3 Bog forest	T4 Bog forest	T5 Bog forest	T6 Bog forest	T7 Bog forest	T8 Bog forest	T9 Bog forest	T10 Bog forest
Acer pseudoplatanus	Herb																		0.10		
Andromeda polifolia	Herb	2.50	0.50		2.50	2.50	0.50	2.50	15.00	15.00	0.50										
Aulacomnium palustre	Moss			0.50				0.50				0.50							0.50		
Bazzania trilobata	Moss																				
Betula pendula	Tree																	62.50			
Betula pendula	Shrub				0.10																
Betula pubescens	Tree											62.50	2.50								15.00
Betula pubescens	Shrub				0.50	0.10															
Calluna vulgaris	Herb	15.00			50.00	0.50		0.10	2.50	0.50	2.50										
Carex rostrata	Herb																				
Dicranella heteromalla	Moss																				
Dicranum scoparium	Moss											0.50	2.50	2.50		15.00		0.50	2.50		
Dryopteris dilatata	Herb																				
Dryopteris expansa	Herb																				
Eriophorum vaginatum	Herb	37.50	0.50	15.00	15.00	15.00	50.00	2.50	25.00	37.50	15.00										
Fagus sylvatica	Herb																				
Frangula alnus	Shrub			0.50			0.10					0.10	15.00	2.50	0.50	2.50	0.10	25.00		5.00	
Frangula alnus	Herb												0.50								
Hylocomium splendens	Moss											2.50	0.50	25.00			0.50				
Leucobryum glaucum	Moss																				
Melampyrum pratense	Herb	0.50		0.50	0.50	0.50	2.50		0.50		2.50										
Molinia caerulea	Herb		15.00	2.50	2.50	2.50	0.50	15.00	5.00	2.50	0.50	15.00	15.00	15.00	15.00	15.00	15.00	15.00	0.50	15.00	5.00
Picea abies	Tree			5.00			25.00	15.00				25.00	75.00	15.00	75.00	87.50	75.00	37.50		62.50	37.50
Picea abies	Herb															0.10					
Picea abies	Shrub																		15.00		
Pinus mugo	Shrub							37.50													
Pinus sylvestris	Tree			5.00																0.50	37.50
Pinus sylvestris	Shrub						0.10														
Plagiochila asplenioides	Moss													15.00	0.10						
Plagiomnium ellipticum	Moss																				
Plagiomnium undulatum	Moss																				
Plagiothecium undulatum	Moss																				
Pleurozium schreberi	Moss			0.50								2.50	37.50	0.50	25.00	37.50	37.50	2.50	15.00	37.50	15.00
Polytrichum formosum	Moss																				
Quercus robur	Herb																				
Rhytidiadelphus loreus	Moss											15.00	0.50	2.50							
Sorbus aucuparia	Shrub															5.00					
Sphagnum angustifolium	Moss	15.00	37.50	62.50	15.00	37.50	50.00	37.50	37.50	37.50	50.00	0.50	2.50	25.00	5.00	5.00	2.50		62.50	15.00	2.50
Sphagnum capillifolium	Moss	2.50	0.50			0.50		2.50	2.50		15.00				0.50						
Sphagnum magellanicum	Moss	62.50	62.50	15.00	15.00	62.50	15.00	62.50	62.50	62.50	37.50	15.00		25.00	50.00	15.00	37.50	25.00	15.00	37.50	75.00
Syntrichia ruralis	Moss																				
Vaccinium myrtillus	Herb	0.50		62.50		15.00	15.00	0.50	2.50			37.50	15.00	62.50	15.00	15.00	37.50	37.50	62.50	62.50	15.00
Vaccinium oxycoccos	Herb	2.50	0.50	2.50	15.00	2.50	2.50	2.50	15.00	25.00	2.50										
Vaccinium uliginosum	Herb										25.00										
Vaccinium vitis-idaea	Herb																2.50				

Species / Plot + Site	Vegetation layer	M1 Mount - Drained bog	M2 Mount - Drained bog	M3 Mount - Drained bog	M4 Mount - Drained bog	M5 Mount - Drained bog	M6 Mount - Drained bog	M7 Mount - Drained bog	M8 Mount - Drained bog	F1 Former surface - Drained bog	F2 Former surface - Drained bog	F3 Former surface - Drained bog	F4 Former surface - Drained bog	F5 Former surface - Drained bog	F6 Former surface - Drained bog	F7 Former surface - Drained bog	F8 Former surface - Drained bog	D1 Draiange ditch - Drained bog	D2 Draiange ditch - Drained bog	D3 Draiange ditch - Drained bog	D4 Draiange ditch - Drained bog	D5 Draiange ditch - Drained bog
Acer pseudoplatanus	Herb																					
Andromeda polifolia	Herb																					
Aulacomnium palustre	Moss																					
Bazzania trilobata	Moss			15.00																		
Betula pendula	Tree							87.50	15.00		2.50											
Betula pendula	Shrub											0.10										
Betula pubescens	Tree			37.50										37.50		15.00	15.00					
Betula pubescens	Shrub				2.50	0.50	0.10		25.00				5.00									
Calluna vulgaris	Herb																					
Carex rostrata	Herb																		15.00			
Dicranella heteromalla	Moss		0.50									0.50					0.50					
Dicranum scoparium	Moss	2.50	0.50	2.50	2.50	2.50	2.50	2.50	15.00			2.50	2.50		2.50	0.50	2.50					
Dryopteris dilatata	Herb				5.00																	
Dryopteris expansa	Herb		0.10																			2.50
Eriophorum vaginatum	Herb										0.10								0.50	15.00		
Fagus sylvatica	Herb													0.10								
Frangula alnus	Shrub				0.50		0.50		2.50	2.50		2.50	0.10		15.00							
Frangula alnus	Herb																0.50					
Hylocomium splendens	Moss			37.50	37.50		15.00			2.50				5.00			2.50					2.50
Leucobryum glaucum	Moss						0.50										0.50					
Melampyrum pratense	Herb																					
Molinia caerulea	Herb				15.00	0.50	0.50		15.00	15.00	2.50	0.50	50.00	15.00	15.00					2.50		0.50
Picea abies	Tree			87.50		62.50	62.50			62.50			62.50	62.50		15.00	62.50					
Picea abies	Herb					25.00				0.10		0.50			0.10	0.50	2.50					
Picea abies	Shrub	50.00	75.00	0.50			37.50		15.00													
Pinus mugo	Shrub																					
Pinus sylvestris	Tree	25.00									25.00	25.00	15.00			37.50						
Pinus sylvestris	Shrub																					
Plagiochila asplenioides	Moss																					
Plagiomnium ellipticum	Moss															0.50						
Plagiomnium undulatum	Moss				0.50																	
Plagiothecium undulatum	Moss														2.50							
Pleurozium schreberi	Moss	50.00	25.00	37.50	25.00	15.00	50.00	37.50	25.00	0.50	15.00	15.00	50.00	5.00	5.00	2.50	15.00					0.50
Polytrichum formosum	Moss	0.50	2.50		2.50	0.50											0.50					0.50
Quercus robur	Herb			0.10		0.10										0.10						0.10
Rhytidiadelphus loreus	Moss	0.50	2.50	0.50	0.50	75.00	0.50	0.50	2.50					2.50	0.50	0.50	2.50					
Sorbus aucuparia	Shrub				2.50												2.50					
Sphagnum angustifolium	Moss				2.50				25.00	2.50	75.00	62.50	2.50	0.50	2.50	0.50		87.50	87.50	50.00	87.50	75.00
Sphagnum capillifolium	Moss																					
Sphagnum magellanicum	Moss	2.50	25.00						25.00	62.50		15.00	2.50	50.00	25.00	50.00	37.50			50.00	2.50	
Syntrichia ruralis	Moss							0.10														
Vaccinium myrtillus	Herb	5.00	15.00	75.00	37.50	37.50	15.00	75.00	62.50	15.00	50.00	62.50	25.00	2.50	37.50	50.00	25.00			15.00		0.50
Vaccinium oxycoccos	Herb																					
Vaccinium uliginosum	Herb																					
Vaccinium vitis-idaea	Herb																					

Coverage rates of species [%] of survey in August

Species / Plot + Site	Vegetation layer	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10
		Open bog	Open bog	Open bog	Open bog	Open bog	Open bog	Open bog	Open bog	Open bog	Open bog	Bog forest	Bog forest	Bog forest	Bog forest	Bog forest	Bog forest	Bog forest	Bog forest	Bog forest	Bog forest
Acer pseudoplatanus	Herb																		0.10		
Andromeda polifolia	Herb	5.00	0.50		2.50	2.50	0.50	1.50	5.00	15.00	0.50										
Aulacomnium palustre	Moss			0.50				0.50				0.50							0.50		
Bazzania trilobata	Moss																				
Betula pendula	Tree																	62.50			
Betula pendula	Shrub				0.10																
Betula pubescens	Tree											62.50	2.50								15.00
Betula pubescens	Shrub				0.50	0.10															
Calluna vulgaris	Herb	15.00			50.00	2.50			0.50	0.50	5.00										
Carex rostrata	Herb																				
Dicranella heteromalla	Moss																				
Dicranum scoparium	Moss											0.50	2.50	2.50		15.00		0.50	2.50		
Dryopteris dilatata	Herb																				
Dryopteris expansa	Herb																				
Eriophorum vaginatum	Herb	25.00	1.50	15.00	25.00	15.00	37.50	5.00	15.00	15.00	15.00										
Fagus sylvatica	Herb																				
Frangula alnus	Shrub			2.50			0.10					0.10	15.00	2.50	0.50	2.50	0.10	25.00		15.00	
Frangula alnus	Herb												0.50								
Hylocomium splendens	Moss											2.50	0.50	25.00			0.50				
Leucobryum glaucum	Moss																				
Melampyrum pratense	Herb	0.50			0.50	0.50	0.50		0.50		2.50										
Molinia caerulea	Herb		25.00	15.00	5.00	15.00	1.50	15.00	25.00	25.00	2.50	25.00	50.00	37.50	37.50	25.00	15.00	37.50	2.50	37.50	15.00
Picea abies	Tree			5.00			25.00	15.00				25.00	75.00	15.00	75.00	87.50	75.00	37.50		62.50	37.50
Picea abies	Herb															0.10					
Picea abies	Shrub																		15.00		
Pinus mugo	Shrub							37.50													
Pinus sylvestris	Tree			5.00																0.50	37.50
Pinus sylvestris	Shrub						0.10														
Plagiochila asplenioides	Moss													15.00	0.10						
Plagiomnium ellipticum	Moss																				
Plagiomnium undulatum	Moss																				
Plagiothecium undulatum	Moss																				
Pleurozium schreberi	Moss			0.50								2.50	37.50	0.50	25.00	37.50	37.50	2.50	15.00	37.50	15.00
Polytrichum formosum	Moss																				
Quercus robur	Herb																				
Rhytidiadelphus loreus	Moss											15.00	0.50	2.50							
Sorbus aucuparia	Shrub															2.50					
Sphagnum angustifolium	Moss	15.00	37.50	62.50	15.00	37.50	50.00	37.50	37.50	37.50	50.00	0.50	2.50	25.00	5.00	5.00	2.50		62.50	15.00	2.50
Sphagnum capillifolium	Moss	2.50	0.50			0.50		2.50	2.50		15.00				0.50						
Sphagnum magellanicum	Moss	62.50	62.50	15.00	15.00	62.50	15.00	62.50	62.50	62.50	37.50	15.00		25.00	50.00	15.00	37.50	25.00	15.00	37.50	75.00
Syntrichia ruralis	Moss																				
Vaccinium myrtillus	Herb	0.50		62.50		15.00	15.00	0.50	2.50			25.00	5.00	37.50	5.00	5.00	15.00	15.00	25.00	37.50	5.00
Vaccinium oxycoccos	Herb	2.50	2.50	2.50	5.00	2.50	2.50	2.50	5.00	37.50	2.50										
Vaccinium uliginosum	Herb										25.00										
Vaccinium vitis-idaea	Herb																2.50				

Species / Plot + Site	Vegetation layer	M1	M2	M3	M4	M5	M6	M7	M8	F1	F2	F3	F4	F5	F6	F7	F8	D1	D2	D3	D4	D5
		Mount - Drained bog	Mount - Drained bog	Mount - Drained bog	Mount - Drained bog	Mount - Drained bog	Mount - Drained bog	Mount - Drained bog	Mount - Drained bog	Former surface - Drained bog	Former surface - Drained bog	Former surface - Drained bog	Former surface - Drained bog	Former surface - Drained bog	Former surface - Drained bog	Former surface - Drained bog	Former surface - Drained bog	Draiange ditch - Drained bog	Draiange ditch - Drained bog	Draiange ditch - Drained bog	Draiange ditch - Drained bog	Draiange ditch - Drained bog
Acer pseudoplatanus	Herb																					
Andromeda polifolia	Herb																					
Aulacomnium palustre	Moss																					
Bazzania trilobata	Moss			15.00																		
Betula pendula	Tree							87.50	15.00		2.50											
Betula pendula	Shrub											0.10										
Betula pubescens	Tree			37.50										37.50		15.00	15.00					
Betula pubescens	Shrub				2.50	0.50	0.10		25.00				5.00									
Calluna vulgaris	Herb																					
Carex rostrata	Herb																		15.00			
Dicranella heteromalla	Moss		0.50									0.50					0.50					
Dicranum scoparium	Moss	2.50	0.50	2.50	2.50	2.50	2.50	2.50	15.00			2.50	2.50		2.50	0.50	2.50					
Dryopteris dilatata	Herb				5.00																	
Dryopteris expansa	Herb		0.10																			2.50
Eriophorum vaginatum	Herb										0.10								0.50	25.00		
Fagus sylvatica	Herb													0.10								
Frangula alnus	Shrub				0.50		0.50		2.50	2.50		2.50	0.10		15.00							
Frangula alnus	Herb																0.50					
Hylocomium splendens	Moss			37.50	37.50		15.00			2.50				5.00			2.50					2.50
Leucobryum glaucum	Moss						0.50										0.50					
Melampyrum pratense	Herb																					
Molinia caerulea	Herb				37.50	0.50	2.50		37.50	37.50	5.00	5.00	87.50	37.50	50.00					15.00		2.50
Picea abies	Tree			87.50		62.50	62.50			62.50			62.50	62.50		15.00	62.50					
Picea abies	Herb					25.00				0.10		0.50			0.10	0.50	2.50					
Picea abies	Shrub	50.00	75.00	0.50			37.50		15.00													
Pinus mugo	Shrub																					
Pinus sylvestris	Tree	25.00									25.00	25.00	15.00			37.50						
Pinus sylvestris	Shrub																					
Plagiochila asplenioides	Moss																					
Plagiomnium ellipticum	Moss															0.50						
Plagiomnium undulatum	Moss				0.50																	
Plagiothecium undulatum	Moss														2.50							
Pleurozium schreberi	Moss	50.00	25.00	37.50	25.00	15.00	50.00	37.50	25.00	0.50	15.00	15.00	50.00	5.00	5.00	2.50	15.00					0.50
Polytrichum formosum	Moss	0.50	2.50		2.50	0.50											0.50					0.50
Quercus robur	Herb			0.10		0.10										0.10						0.10
Rhytidiadelphus loreus	Moss	0.50	2.50	0.50	0.50	75.00	0.50	0.50	2.50					2.50	0.50	0.50	2.50					
Sorbus aucuparia	Shrub				2.50												2.50					
Sphagnum angustifolium	Moss				2.50				25.00	2.50	75.00	62.50	2.50	0.50	2.50	0.50		87.50	87.50	50.00	87.50	75.00
Sphagnum capillifolium	Moss																					
Sphagnum magellanicum	Moss	2.50	25.00						25.00	62.50		15.00	2.50	50.00	25.00	50.00	37.50			50.00	2.50	
Syntrichia ruralis	Moss							0.10														
Vaccinium myrtillus	Herb	2.50	15.00	50.00	15.00	5.00	5.00	62.50	25.00	5.00	25.00	37.50	5.00	2.50	15.00	25.00	5.00			15.00		0.50
Vaccinium oxycoccos	Herb																					
Vaccinium uliginosum	Herb																					
Vaccinium vitis-idaea	Herb																					

E) Environmental data

Plot_ID	Site/Feature	Gravimetric water content [%]	Decomposition (Von Post)	pH	Canopy density (estimated)
B1	Open bog	0.922	H3	3.44	0.0%
B2	Open bog	0.943	H2	3.45	0.0%
B3	Open bog	0.899	H3	3.38	10.0%
B4	Open bog	0.929	H4	3.35	0.0%
B5	Open bog	0.928	H3	3.66	0.0%
B6	Open bog	0.921	H3	3.09	25.0%
B7	Open bog	0.944	H2	3.51	40.0%
B8	Open bog	0.943	H2	3.64	0.0%
B9	Open bog	0.937	H2	3.58	0.0%
B10	Open bog	0.910	H4	3.5	0.0%
T1	Bog forest	0.891	H6	3.34	90.0%
T2	Bog forest	0.897	H7	3.2	80.0%
T3	Bog forest	0.889	H6	3.21	15.0%
T4	Bog forest	0.892	H3	3.31	60.0%
T5	Bog forest	0.865	H4	3.26	90.0%
T6	Bog forest	0.903	H7	3.28	70.0%
T7	Bog forest	0.894	H7	3.13	90.0%
T8	Bog forest	0.912	H3	3.61	10.0%
T9	Bog forest	0.907	H6	3.29	60.0%
T10	Bog forest	0.905	H7	3.31	80.0%
M1	Mount	0.764	H9	3.45	30.0%
M2	Mount	0.782	H10	3.34	0.0%
M3	Mount	0.767	H9	3.32	70.0%
M4	Mount	0.738	H8	3.78	0.0%
M5	Mount	0.651	H9	3.85	80.0%
M6	Mount	0.754	H10	3.76	70.0%
M7	Mount	0.812	H8	3.54	70.0%
M8	Mount	0.818	H10	3.28	40.0%
F1	Former surface	0.898	H8	3.23	60.0%
F2	Former surface	0.908	H7	3.29	30.0%
F3	Former surface	0.819	H5	3.61	30.0%
F4	Former surface	0.878	H7	3.42	50.0%
F5	Former surface	0.874	H7	3.35	70.0%
F6	Former surface	0.895	H8	3.52	10.0%
F7	Former surface	0.916	H7	3.23	80.0%
F8	Former surface	0.880	H7	3.31	70.0%
D1	Draiange ditch	0.948	H2	3.69	80.0%
D2	Draiange ditch	0.955	H3	3.51	10.0%
D3	Draiange ditch	0.949	H2	3.46	0.0%
D4	Draiange ditch	0.938	H3	3.53	20.0%
D5	Draiange ditch	0.936	H3	3.62	30.0%

F) Description of the used indicator value scales for vascular plants and bryophytes (Landolt et al., 2010)

Climate indicators for vascular plants and bryophytes:

Temperature (T)	
1	alpine and nival
1.5	lower alpine, supra subalpine and upper subalpine
2	subalpine
2.5	lower subalpine and upper montane
3	montane
3.5	lower montane and upper colline
4	colline
4.5	warm colline
5	very warm colline

Light (L)	
1	deep shade: plant tolerates even less than 3% of relative illumination
2	shade: plant rarely tolerates below 3%, but often below 10% of relative illumination
3	semi-shade: plant rarely tolerates below 10% of relative illumination
4	well lit places: plant tolerates light shade only occasionally or for short periods
5	full light: plant grows only in open and sunny places

Soil indicators for vascular plants:

Moisture (F)	
1	very dry
1.5	dry
2	moderately dry
2.5	fresh
3	moderately moist
3.5	moist
4	very moist
4.5	wet
5	flooded, i.e. submerged

Reaction (R)	
1	extremely acid: pH 2.5-5.5 (exclusively having range I)
2	acid: pH 3.5-6.5 (ranging between 2.5-7.5)
3	weakly acid to weakly neutral: pH 4.5-7.5 (ranging between 3.5-8.5)

4	neutral or alkaline: pH 5.5-8.5 (ranging between 4.5-8.5)
5	alkaline, high pH: pH 6.5-8.5 (exlusively having range I)
-	no indication for species that do not thrive in water or on soil, or species having a wide variation range X

Nutrients (N)	
1	very infertile
2	infertile
3	medium infertile to medium fertile
4	fertile
5	very fertile and over-rich
-	no indication for species that grow neither in the water nor on the soil or plants attributed by X (wide range of variation)

Humus (H)	
1	little or no humus
3	moderate humus content (mostly as mull)
5	high humus content (mostly as raw humus, moder or peat)
-	no indication for species that do not root in the soil or plants attributed by X (wide range of variation)

Soil indicators for bryophytes:

Moisture (F)	
1	very dry (exposed substrates in regions with low precipitation or in places protected from rain)
2	dry (exposed substrates in places with low humidity (mostly rocks) or ground in regions with low precipitation)
3	mesic (medium moisture conditions)
4	moist (substrate drying out only rarely, though hardly ever submerged)
5	wet (substrate never dry but frequently or permanently submerged)

Reaction (R)	
1	very acid (substrate pH < ca. 4, e.g. raised bog peat)
2	acid (substrate pH ca. 3.5-5, e.g. rotten wood)
3	subneutral (base-poor; substrate pH ca. 4.5-6.5, e.g. silicious rock affected by lime)
4	± neutral (substrate pH ca. 6-7.5, e.g. many soils in deciduous forests)
5	alkaline (substrate pH > ca. 7, e.g. limestone)

Nutrients (N)

1	infertile substrates (poor in nutrients, e.g. silicious rock or peat)
3	intermediate substrates (e.g. forest soil or moderately fertilized meadow soil)
5	fertile substrates (rich in nutrients, e.g. rock or tree branches fertilized by birds)

Humus (H)	
1	humus-poor (little or no humus in the soil)
3	moderate humus content (mostly mull)
5	humus-rich (mostly raw humus, moder or peat)