



Reviews and syntheses: When does moss act as a methane biofilter?

Transport pathways and environmental controls in peatlands

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10 **Abstract.** Peatlands are critical global carbon stores and the largest natural source of atmospheric methane (CH_4). Bryophytes, particularly *Sphagnum* and submerged brown mosses, can act as effective biological CH_4 filters by hosting methanotrophs within their hydrated tissues and providing photosynthetically derived oxygen. In diffusion-dominated systems, moss-associated oxidation can consume 61–99% of upward CH_4 flux. However, the presence of moss cover alone does not guarantee ecosystem-scale emission reduction. Synthesizing evidence from 122 studies across field observations, 15 mesocosms, and manipulation experiments, we evaluate the moss biofilter as a realized, state-dependent transport-and-oxidation process. We show that biofilter effectiveness emerges from competition among three distinct pathways: diffusion through the living moss layer, vascular-plant bypass via aerenchyma, and episodic ebullition. Only the diffusive fraction is consistently exposed to the moss oxidation zone. This pathway partitioning is shaped by microtopography and successional trajectories and is highly vulnerable to global-change stressors. Hydrology acts as the master regulator: modest water-table 20 drawdown expands the oxic oxidation layer, whereas severe desiccation damages moss structure and microbial habitats. Furthermore, warming and chronic nitrogen enrichment can destabilize moss–methanotroph metabolic coupling and promote graminoid expansion, exacerbating vascular bypass. For peatland management and paludiculture, hydrological rewetting is necessary but insufficient; without rapid re-establishment of a functional moss layer and mitigation of nutrient legacies, rewetted sites can become bypass-dominated CH_4 hotspots. Techniques such as topsoil removal and the moss layer transfer 25 technique (MLTT) can accelerate recovery, provided full CO_2 – CH_4 trade-offs are evaluated. Finally, we highlight priorities for Earth system modeling, emphasizing that models must explicitly separate diffusive, vascular, and ebullitive pathways rather than treating moss cover as a static oxidation parameter.



Keywords: methane oxidation; methanotrophs; *Sphagnum*; bryophytes; peatland restoration; vascular-plant aerenchyma;
 ebullition; winter methane cycling; paludiculture

Introduction

Methane (CH₄) is a potent, short-lived climate pollutant and a major contributor to contemporary warming (Nisbet et al., 2019; IPCC, 2021; WMO, 2025). Atmospheric CH₄ concentrations have continued to rise, increasing the urgency of
 constraining natural and anthropogenic sources. Wetlands are the largest natural CH₄ source and contribute roughly one-third
 of global CH₄ emissions, while peatlands store a substantial fraction of terrestrial soil carbon (Nichols & Peteet, 2019;
 Saunio et al., 2020). The processes regulating CH₄ production, oxidation, and transport in peatlands are therefore central to
 projections of climate–carbon feedback and to the design of climate-effective restoration.

Bryophytes, particularly *Sphagnum* mosses, can regulate peatland CH₄ cycling by hosting CH₄-oxidizing
 microorganisms on moss surfaces and within water-filled hyaline cells (Larmola et al., 2010; Kip et al., 2012). Mosses
 provide a hydrated microbial habitat, and photosynthesis by living tissues supplies O₂ that supports aerobic methanotrophy
 near the peat–moss interface (Larmola et al., 2010; Kip et al., 2012). Where CH₄ transport is predominantly diffusive,
 associated methanotrophs can consume a large fraction of the upward flux; oxidation reached 61–99% of sediment-produced
 CH₄ in some moss-dominated systems (Knoblauch et al., 2015). Moss communities can thus function as biological CH₄
 filters while coupling methane-derived carbon and, in some cases, nitrogen to peatland nutrient cycling.

This climate-regulating function cannot be inferred from moss abundance alone. The route by which CH₄ reaches
 the atmosphere determines whether it encounters the oxidative moss layer. Aerenchymatous sedges and grasses can transport
 CH₄ directly from anoxic peat to the atmosphere, bypassing surface oxidation (Stephen et al., 1998; King et al., 1998).
 Ebullition likewise releases CH₄ rapidly through bubbles and preferential pathways, allowing little contact with moss-
 associated methanotrophs (Cooper et al., 2014; Bieniada & Strack, 2021). Moss-filter effectiveness therefore emerges from
 competition among diffusion through moss, vascular transport, and ebullitive release.

Global change is altering this pathway balance. Hydrological change determines whether mosses remain hydrated
 and active or cross drought thresholds that impair host physiology and microbial habitat. Warming and nitrogen enrichment
 can modify microbial coupling, nutrient supply, and vegetation composition, potentially favoring graminoids and their
 efficient vascular transport pathways (Petro et al., 2023; Lu et al., 2025). Permafrost thaw and subsequent succession further
 show that CH₄ flux reflects not only production but also the development or loss of a surface oxidation layer (Turetsky et al.,
 2020; Heffernan et al., 2022). Robust prediction therefore requires identifying when peatlands remain moss filtered and
 when they become bypass dominated.

Previous reviews have synthesized wetland CH₄ microbiology, plant-mediated transport, and restoration outcomes
 (Darusman et al., 2023; Ge et al., 2024), but these components are often treated separately. Consequently, it remains difficult
 to predict how moss-associated oxidation interacts with competing transport pathways across ecological gradients and under



global change. An integrative framework is needed to connect microbial capacity, vegetation architecture, environmental stress, and management intervention.

Two distinctions delimit this framework. First, a moss biofilter is a realized ecosystem function, not simply a potential oxidation rate measured after incubating moss under favorable CH₄ and O₂ concentrations. Realized attenuation requires both delivery of CH₄ to the living moss layer and oxidation during its residence there. Second, the evidence base is taxonomically and geographically uneven. Direct demonstrations are concentrated in northern *Sphagnum* peatlands and submerged Arctic brown-moss systems, with fewer process studies from Patagonia and little comparable evidence from tropical peatlands or other bryophyte assemblages (Liebner et al., 2011; Kip et al., 2012). Feather-moss stands can even support methanogenesis and low but measurable CH₄ release under some conditions (Kanaparthi et al., 2017). We therefore treat biofilter strength as a host-, habitat-, and pathway-specific property rather than a universal consequence of moss cover.

Here, we evaluate the moss biofilter as a state-dependent transport-and-oxidation process. We (1) synthesize the mechanistic basis of moss-associated CH₄ oxidation and carbon–nitrogen coupling; (2) assess how vegetation composition, succession, microtopography, and transport pathways determine whether CH₄ is filtered or bypassed; (3) examine how global-change drivers affect biofilter persistence; (4) derive implications for peatland restoration and management; and (5) identify priorities for representing pathway-dependent moss effects in ecosystem and Earth system models.

2 Methodology

The search, screening, and reporting procedures for this structured narrative review followed applicable PRISMA 2020 principles to improve transparency and reproducibility (Page et al., 2021).

2.1 Information sources and search strategy

Web of Science Core Collection and Scopus were searched in June 2026 from database inception through June 2026. The primary search string, applied to titles, abstracts, and keywords, was (“moss*” OR “*Sphagnum*” OR “bryophyte*”) AND (“methane” OR “CH₄” OR “methanotroph*” OR “methanogenesis” OR “greenhouse gas”). Reference lists of key reviews and meta-analyses were screened manually. Targeted searches additionally addressed aerenchyma and plant-mediated transport, ebullition, rewetting, *Sphagnum* farming, underrepresented climatic regions and moss types, winter and freeze–thaw processes, permafrost thaw, and anaerobic CH₄ oxidation. Complete search strings and thematic blocks are provided in Supplementary Table S1.

2.2 Eligibility criteria

Eligible studies examined terrestrial or aquatic ecosystems containing moss layers and reported CH₄ flux or oxidation, methanotroph composition or functional genes, isotopic evidence, or responses to environmental drivers or restoration. Field observations, mesocosms, incubations, and manipulative experiments were included; comparisons among moss-dominated, vascular-plant-dominated, bare-peat, and control conditions were retained where available. Studies focused exclusively on vascular plants or non-bryophyte aquatic producers, grey literature, conference abstracts without full data, and non-English publications were excluded.



2.3 Selection process and data extraction

The search identified 412 records. After removal of 114 duplicates, 298 titles and abstracts were screened and 174 articles underwent full-text assessment. In total, 122 studies met the eligibility criteria and entered the qualitative synthesis (Figure 2; Supplementary Table S1). Because study designs, temporal scales, and reporting units were highly heterogeneous, a quantitative meta-analysis was not warranted. Evidence was instead organized around biological mechanisms, ecological pathway competition, environmental stressors, and restoration applications.

2.4 Evidence appraisal and synthesis limitations

For each included study, we recorded ecosystem and region, bryophyte host or moss functional type, vascular-plant composition, microform, hydrological state, season, experimental design, spatial and temporal scale, inferred transport pathway, and the reported CH₄ production, oxidation, or surface flux. Isotopic transfer, manipulative flux partitioning, functional-gene or transcript evidence, and microenvironmental profiles were coded separately. Quantitative values were retained only when the measurement basis, units, and system boundary were sufficiently clear. Because rates reported for intact ecosystems, excised moss, sediments, and potential incubations are not directly commensurable, numerical examples are used to establish plausible magnitudes and contrasts rather than pooled as a common effect size.

We also assessed four recurrent sources of inference bias: geographic concentration in Northern Hemisphere *Sphagnum* systems; seasonal bias toward growing-season measurements; method dependence arising from chambers, incubations, isotopes, and molecular proxies; and confounding of transport, production, and oxidation in vegetation-removal or water-table experiments. A formal study-level risk-of-bias score was not applied because the evidence spans fundamentally different designs and outcomes. Conclusions are instead calibrated to the evidence hierarchy described below, and study-specific rates are not interpreted as globally transferable performance ranges.

3 Mechanistic basis of moss-mediated methane oxidation

The moss biofilter is a coupled physical–biological system in which mosses regulate CH₄ transport and O₂ availability, while associated methanotrophs consume CH₄ before atmospheric release. Their interaction creates an oxidation zone at the peat–moss interface, where CH₄ fate depends on substrate supply, O₂ availability, and microbial activity (Larmola et al., 2010; Kip et al., 2012). Filtering is strongest when CH₄ diffuses through this zone and weakest when vascular transport or ebullition bypasses it (Figure 1).

Conceptually, realized attenuation can be decomposed into two terms: the fraction of upward CH₄ routed through the moss layer and the oxidation efficiency applied to that routed fraction. A site can therefore contain highly active methanotrophs yet emit strongly if most CH₄ leaves through aerenchyma or bubbles. Conversely, modest potential oxidation may have a large ecosystem effect where nearly all transport is diffusive. This decomposition provides the organizing logic for separating microbial capacity from pathway exposure throughout the review.

We distinguish four levels of evidence for the moss-biofilter mechanism: (1) direct isotopic evidence of carbon or nitrogen transfer between methanotrophs and mosses; (2) manipulative evidence of altered CH₄ oxidation or emission; (3)



130 molecular evidence identifying functional microbial groups; and (4) microenvironmental evidence describing CH₄ and O₂ gradients within moss tissues. This hierarchy separates well-supported mechanisms from plausible but incompletely quantified processes; the corresponding pathways and confidence assessments are summarized in Table 1.

3.1 The moss microenvironment: creating an oxidation zone

135 CH₄ oxidation is spatially constrained by steep, opposing gradients of CH₄ and O₂ within the moss layer. CH₄ diffuses upward from anoxic peat or water-saturated sediment, whereas O₂ enters from the atmosphere and is produced by photosynthetically active moss tissues. Their overlap creates a narrow interface in which both substrates are available for aerobic methanotrophy.

Direct profiling supports this interfacial interpretation but also shows that the oxidation zone has no universal depth. Membrane-inlet mass spectrometry, O₂ microelectrodes, and confocal observations in peat monoliths resolved sharp vertical
 140 separation between oxygenated surface activity and deeper anaerobic processes over centimetre scales (Lloyd et al., 1998a,b). The position and thickness of this overlap zone shift with water-table position, moss density, temperature, irradiance, and gas consumption. Measurements made at only one nominal depth can therefore miss the active interface or misattribute peat oxidation to the living moss tissue.

Moss architecture helps maintain this interface. Methanotrophs occur on moss surfaces and within the dead, water-
 145 storage hyaline cells of *Sphagnum*, which provide a hydrated and comparatively protected microbial habitat (Kip et al., 2012). Mesocosm evidence further shows that submerged *Sphagnum* can sustain abundant CH₄ oxidizers and sharply reduce CH₄ emission when diffusion directs the gas through the moss layer (Kox et al., 2021). Photosynthetic O₂ production occurs in living chlorophyllous tissues, whereas the hyaline-cell network retains the water needed to maintain host–microbe contact.

The importance of pathway exposure is demonstrated by Knoblauch et al. (2015): submerged moss layers oxidized
 150 61–99% of sediment-produced CH₄ where transport was predominantly diffusive, but the oxidized fraction declined when vascular plants provided a bypass. Moss-filter performance therefore depends on both microbial capacity and the route through which CH₄ reaches the surface. Representative rates and oxidation fractions across contrasting moss-bearing ecosystems are compiled in Table 2.

This review defines the moss biofilter strictly as aerobic oxidation within or immediately adjacent to living moss.
 155 Anaerobic oxidation of methane (AOM) in deeper, anoxic peat is a distinct sink that may act in series with the surface filter. Moss cover could influence AOM indirectly by maintaining wetness or supplying redox-active organic matter, but available evidence does not yet justify assigning subsurface AOM to moss activity itself (Valenzuela et al., 2019; Zhao & Lu, 2023). Production, AOM, aerobic peat oxidation, and moss-associated oxidation should consequently be quantified as separate terms whenever the data permit.

160 3.2 Methanotrophic partners: the microbial engine of the biofilter

Moss-associated methanotrophs convert CH₄ to the less radiatively active carbon dioxide (CO₂). Molecular surveys consistently identify Type II methanotrophs, including *Methylocystis* and related lineages, as important constituents of



Sphagnum-associated communities, while Type I methanotrophs may contribute in wetter, CH₄-rich habitats (Kip et al., 2012; Xiang et al., 2014).

Their ecological importance lies in functional traits suited to nutrient-poor peatlands, including activity at low CH₄ concentrations and, for some taxa, diazotrophy. Kolton et al. (2022), for example, identified diazotrophic methanotrophs, including *Methyloferula*, within the *Sphagnum* core microbiome across North American peatlands. These organisms connect CH₄ oxidation with nitrogen acquisition and can contribute to the persistence of the oxidation layer; they are therefore better understood as functional partners of the moss host than as methane consumers alone.

Inference about this guild is sensitive to marker choice. Surveys based only on *pmoA* can miss methanotrophs such as *Methyloferula stellata*, which lacks particulate methane monooxygenase and relies on soluble methane monooxygenase encoded by *mmoX* (Dedysh et al., 2015). Conversely, detection of 16S rRNA genes, *pmoA*, *mmoX*, or *nifH* establishes metabolic potential or community presence, not the rate operating in situ. Host-species comparisons further show that bacterial diversity and CH₄ oxidation can vary independently (Wang et al., 2024). Strong attribution therefore requires combining community profiling with transcripts, stable-isotope incorporation, or process-rate measurements.

3.3 Carbon and nitrogen coupling: from methane oxidation to ecosystem feedback

The moss–methanotroph association extends beyond CH₄ removal because methane-derived carbon and microbially fixed nitrogen can be retained within the system. Stable-isotope experiments demonstrate incorporation of CH₄-derived carbon into *Sphagnum* biomass, indicating that methanotrophy can supplement host carbon acquisition in nutrient-poor peatlands (Larmola et al., 2010).

Carbon transfer may involve both refixation of CO₂ produced during CH₄ oxidation and assimilation of microbial-derived compounds. In submerged brown-moss systems, Liebner et al. (2011) detected CH₄-derived carbon in microbial biomarkers and moss sterols, providing direct evidence that methanotrophy contributes to host-associated carbon cycling.

The association can also affect nitrogen supply. Some moss-associated methanotrophs possess nitrogen-fixing capacity, a potentially important trait in nutrient-limited peatlands. Methanotrophy stimulated nitrogen fixation during peatland development (Larmola et al., 2014), and combined genomic and isotopic evidence implicates diazotrophic methanotrophs in both CH₄ and nitrogen cycling (Kolton et al., 2022).

This coupling is environmentally vulnerable. Experimental warming altered surface-peat microbial communities and decoupled CH₄ oxidation from nitrogen fixation, even as methanotrophic activity increased (Petro et al., 2023). Biofilter persistence may therefore depend not only on short-term oxidation rates but also on the nutrient feedback that sustains moss growth.

The mutualistic interpretation should nevertheless remain conditional. Isotope studies have attributed approximately 10–30% of *Sphagnum* biomass carbon to recycled CH₄ under particular wet, CH₄-rich conditions (Raghoebarsing et al., 2005; Larmola et al., 2010), but that contribution need not apply to aerated hummocks or substrate-limited sites. Likewise, added CH₄ did not stimulate N₂ fixation in every *Sphagnum* assemblage, and non-methanotrophic diazotrophs can dominate



nitrogen input (Leppänen et al., 2015). Demonstrating CH₄ oxidation is therefore insufficient to infer a reciprocal host benefit; carbon transfer, nitrogen transfer, and effects on moss performance must be evaluated independently.

Carbon fate after oxidation also matters. Conversion of CH₄ to CO₂ sharply reduces radiative forcing per mole of carbon, but it does not by itself demonstrate additional peat accumulation. The CO₂ may be refixed by moss, respired back to the atmosphere, dissolved and transported, or incorporated into microbial biomass. A complete assessment of the association should therefore distinguish gross CH₄ oxidation from net methane-derived carbon retention and from any longer-term effect on peat formation.

3.4 Physiological regulation: when the biofilter is active

Moss-filter activity depends on the environmental controls of host photosynthesis, hydration, gas diffusion, and microbial metabolism. Unlike vascular plants, mosses lack specialized internal gas-transport tissues; CH₄ exposure and O₂ supply therefore depend largely on diffusion and local photosynthetic activity.

Light is a particularly strong regulator because photosynthesis supplies O₂ within moss tissues. Illumination increased CH₄ oxidation approximately fivefold and nitrogen fixation threefold in *Sphagnum* (Kox et al., 2020). In submerged brown-moss communities, daylight likewise shifted net exchange toward CH₄ uptake, whereas darkness favored emission (Liebner et al., 2011).

The response remains context dependent. Adequate light can strengthen oxidation by increasing O₂ availability, whereas shading by vascular plants, shrubs, algal mats, or snow can suppress photosynthesis. The effect also depends on CH₄ supply and hydration, making light a conditional regulator rather than an independent predictor of ecosystem CH₄ flux.

Light is also a measurement variable. Opaque chambers suppress photosynthesis while changing surface temperature and gas diffusion, so their fluxes are not directly equivalent to measurements made with transparent chambers. Differences between chamber types can be strongest on photosynthetically active hummocks and negligible in wetter hollows (Daulat & Clymo, 1998; Luan & Wu, 2014). Paired light-dark measurements should therefore record moss temperature, irradiance, and O₂ status rather than treating chamber opacity as a purely technical choice.

4 Ecological controls: vegetation structure determines whether methane is filtered or bypassed

Moss-filter effectiveness depends on the pathway by which CH₄ reaches the atmosphere. Across peatland landscapes, vegetation composition, succession, and microtopography regulate the relative contributions of diffusion through moss, transport through vascular-plant aerenchyma, and ebullitive bubble release (Figure 1). Only the diffusive fraction is consistently exposed to the moss-associated oxidation zone.

4.1 Vegetation-mediated pathway competition: moss filter versus vascular shunt

Vegetation structure is a major ecosystem-scale control on CH₄ emission because plant functional types differ fundamentally in gas transport. Moss-dominated surfaces slow diffusive CH₄ movement and can increase residence time within oxygenated tissues. By contrast, aerenchymatous sedges and grasses provide low-resistance conduits between anoxic peat and the atmosphere.



230 This vascular shunt can substantially reduce contact between CH₄ and the surface oxidation zone. Root-mediated gas-transport experiments demonstrate rapid movement through specialized plant tissues (Stephen et al., 1998). Sedge-removal experiments in Arctic wetlands also reduced CH₄ emission, consistent with a decline in plant-mediated transport and associated plant effects on CH₄ production (King et al., 1998). The result should not be interpreted as a transport effect alone, because plant removal can also alter substrate supply and rhizosphere oxidation.

235 The pathway contrast is particularly clear in submerged systems. Knoblauch et al. (2015) found that brown mosses oxidized 61–99% of sediment-produced CH₄ in ponds lacking vascular plants, whereas plant colonization reduced the fraction exposed to moss-associated oxidation by introducing an aerenchymatous bypass.

At ecosystem scales, the magnitude of plant-mediated flux varies with species identity, biomass, and hydrology. Vegetation removal and water-level manipulations in a boreal fen showed that vascular plants strongly regulate CH₄ dynamics (Riutta et al., 2020), and species-specific differences in aerenchyma transport influenced flux across a boreal peatland complex (Korrensalo et al., 2022). Graminoid expansion therefore changes not only community composition but also the architecture of CH₄ transport, potentially weakening moss filtering even where oxidation potential remains high.

240 The available partitioning data show why plant cover alone is an inadequate model proxy. Under natural water levels, vegetation-mediated flux accounted for 68–78% of mean growing-season CH₄ exchange in one boreal fen, with sedges responsible for about three-quarters of that component; experimental drawdown reduced total flux to near zero and largely removed the vegetation effect (Riutta et al., 2020). In another peatland complex, *Scheuchzeria palustris* supplied 45% of ecosystem-scale plant transport despite representing only 16% of aerenchymatous leaf area (Korrensalo et al., 2022). Species-specific conductance and hydrological access to CH₄ must therefore complement biomass or cover in pathway models.

250 4.2 Ebullition: a direct bypass of the moss oxidation layer

Ebullition is a second pathway that can circumvent moss-associated methanotrophs. When dissolved CH₄ exceeds solubility, bubbles form and move rapidly through peat, sediment, or preferential flow paths. Their short residence time in oxygenated surface layers limits exposure to aerobic oxidation, so episodic bubble release can remain large despite high potential methanotrophic activity.

255 Ebullition varies with hydrology, peat structure, temperature, atmospheric pressure, and the abundance of open-water features. In restored peatlands, inundated areas and blocked or infilled ditches can become CH₄ hotspots because they concentrate production and provide efficient release pathways (Cooper et al., 2014; Bieniada & Strack, 2021).

Moss cover may indirectly affect ebullition by changing near-surface CH₄ concentrations and physical resistance, but this interaction remains poorly quantified. Simultaneous partitioning of diffusive, vascular, and ebullitive fluxes is therefore essential; total chamber flux alone cannot reveal the fraction accessible to the moss biofilter.

260 Ebullition is also vulnerable to sampling bias because short chamber deployments can miss infrequent, high-magnitude events, while spatially fixed bubble traps may not represent preferential conduits. Studies should report steady and episodic flux separately and combine automated chambers or hydroacoustic/bubble-trap observations with dissolved



CH₄, peat temperature, water level, and atmospheric pressure. Without event-resolving measurements, an apparent increase
 265 in oxidation efficiency may instead reflect unobserved bubble loss (Bieniada & Strack, 2021).

4.3 Succession: ecosystem transition from bypass-dominated to filter-dominated states

Peatland succession provides a long-term illustration of pathway reorganization. Many systems develop from minerotrophic,
 graminoid-rich fens toward ombrotrophic bogs dominated by *Sphagnum*. This trajectory often reduces vascular bypass and
 increases the fraction of CH₄ that must diffuse through a moss layer, although local hydrology and carbon supply can modify
 270 the pattern.

Across successional gradients, graminoid-rich fens commonly emit more CH₄ because nutrient availability supports
 both methanogenesis and vascular transport. Moore et al. (1994) observed increasing emissions from marshes to graminoid-
 rich fens and lower emissions in mature *Sphagnum* bogs. Similarly, CH₄ production potential declined along Finnish fen-
 bog gradients, while the relative importance of oxidation increased in *Sphagnum*-dominated systems (Zhang et al., 2021).

275 The fen-to-bog transition therefore represents a functional reorganization of carbon cycling rather than a vegetation
 change alone. Vegetation turnover co-varies with declining pH, altered organic-matter quality, and restructuring of
 decomposer and methane-cycling communities, all of which influence CH₄ production and oxidation (Juottonen et al., 2022).

This interpretation is relevant to restoration because disturbed peatlands may pass through a high-emission stage
 dominated by vascular plants before a continuous moss layer develops. Recovery of methane-cycling microbial communities
 280 is closely associated with increasing *Sphagnum* abundance in restored cutover peatlands (Putkinen et al., 2018), suggesting
 that accelerating moss establishment may shorten, but does not by itself eliminate, the bypass-dominated phase.

Successional comparisons nevertheless provide weaker causal evidence than manipulative pathway studies. Fen-to-
 bog gradients simultaneously alter water-table regime, pH, nutrient supply, organic-matter quality, methanogen
 communities, and plant transport. Lower CH₄ emission in a mature *Sphagnum* bog cannot therefore be assigned to moss
 285 oxidation alone (Moore et al., 1994; Zhang et al., 2021; Juottonen et al., 2022). Stronger inference requires repeated
 measurements along dated trajectories that partition production, transport, and oxidation while tracking the same
 hydrological and biogeochemical covariates.

4.4 Microtopography: spatial regulation of methane filtering capacity

Peatland surfaces comprise hummocks, lawns, hollows, and pools that differ in water-table position, oxic-zone thickness,
 290 CH₄ supply, and vegetation. This fine-scale heterogeneity produces spatial variation in both oxidation capacity and the
 proportion of flux exposed to mosses.

Elevated hummocks often have deeper O₂ penetration but limited CH₄ supply, whereas wetter hollows and pools
 can sustain high methanotrophic activity because substrate availability is greater. Measurements across *Sphagnum*
 microhabitats confirm that potential oxidation and CH₄ supply need not be spatially aligned (Kip et al., 2012). Consequently,
 295 a microsite with high oxidation potential may still contribute little to landscape-scale CH₄ removal if little CH₄ passes
 through it.



Microtopography also interacts with vegetation. Aerenchymatous plants on lawns or hummocks can bypass otherwise favorable oxidation zones, and water-level effects depend on microsite structure and plant cover. Mesocosm evidence accordingly shows that CH₄ responses emerge from interactions among water level, vegetation, and surface position rather than from water table alone (Dinsmore et al., 2009).

Annual and seasonal rankings of microforms can also diverge. In a rewetted bog, hollows were the largest annual sources, yet hummock emissions exceeded hollow emissions during parts of the vegetation period (Welpelo et al., 2024). Across a boreal fen, soil fertility explained additional variation that could not be reduced to elevation or water-table distance alone (Mikola et al., 2025). Landscape scaling based only on hummock-hollow area can therefore be biased unless vegetation traits, fertility, and season-specific transport are represented.

Together, vegetation composition, succession, microtopography, and ebullition determine whether peatland CH₄ passes through an active moss filter or escapes through bypass pathways (Figure 3). The key ecological variable is therefore not moss cover per se, but the fraction of total CH₄ flux that encounters a hydrated, oxygenated oxidation layer before atmospheric release.

5 Environmental drivers and anthropogenic stressors: when does the moss biofilter persist or collapse?

The moss biofilter is not a fixed ecosystem attribute. Its effectiveness depends on sustained overlap among CH₄ supply, O₂ availability, and methanotrophic activity within a viable moss layer. Global-change drivers affect CH₄ emissions not only by altering production but also by shifting the relative importance of filtered and bypass pathways. The mechanisms, quantitative evidence, and principal uncertainties associated with major environmental controls are synthesized in Table 3.

5.1 Hydrology as the master regulator of methane filtering capacity

Hydrology is the dominant physical regulator of the balance between CH₄ production and oxidation. Water-table position controls both the volume of anoxic peat available for methanogenesis and the thickness and hydration of the oxygenated surface layer in which moss-associated methanotrophs operate.

Moderate lowering of the water table can reduce CH₄ efflux by expanding the oxic zone, provided moss tissues remain hydrated (Daulat & Clymo, 1998). Hydrology can also override vegetation effects by constraining CH₄ supply and oxidation conditions (Riutta et al., 2020). The response is nevertheless nonlinear because progressive drying eventually reduces moss physiological activity and habitat quality.

Severe desiccation can impair photosynthesis, alter moss structure, and damage the microbial habitat. Species-specific moisture thresholds have been identified, below which physiological damage becomes difficult to reverse (Keane et al., 2025a,b). Methanotrophs can recolonize rewetted moss through water-mediated dispersal (Putkinen et al., 2012), but functional recovery ultimately depends on survival and regrowth of the host. Moderate drying may therefore enhance oxidation, whereas extreme drought can collapse the moss filter.

Recovery is asynchronous across components. In transplantation experiments, previously inactive moss acquired measurable methanotrophy within days and its methanotroph community approached that of active moss within weeks



(Putkinen et al., 2012), whereas canopy regrowth and restoration of the original transport architecture can take much longer. Rapid water-table reversals can also generate short gas pulses before production and oxidation restabilize (Dinsmore et al., 2009). These differing time scales create hysteresis: the water table at which a biofilter fails need not equal the condition at which the full moss-microbial-transport system recovers.

335 5.2 Warming and nutrient enrichment: destabilizing moss–microbial feedbacks

Warming affects the moss biofilter through interacting effects on microbial rates, host physiology, hydrology, and vegetation. CH₄ production and oxidation both respond to temperature, but their net effect varies among ecosystem types. A global synthesis estimated a lower temperature sensitivity of CH₄ emission in moss-dominated wetlands ($Q_{10} = 1.71$) than in vascular-plant-dominated wetlands ($Q_{10} = 2.26$), consistent with pathway-dependent warming responses (Li et al., 2024).

340 Warming can also destabilize the nutrient feedbacks that support moss persistence. In a whole-ecosystem warming experiment, methanotrophic activity increased markedly, while nitrogen fixation declined and became decoupled from CH₄ oxidation; severe warming was also associated with extensive *Sphagnum* mortality (Petro et al., 2023). Short-term stimulation of methanotrophy therefore does not necessarily imply long-term stability of the moss–microbe association.

345 Warming should consequently not be assigned a single positive or negative biofilter response. The reported Q_{10} contrast is an emergent ecosystem relationship, not an isolated temperature response of moss methanotrophs. Direct kinetic stimulation can be outweighed by water-table decline, surface drying, increased methanogenesis, host mortality, or a shift toward vascular plants; under persistently wet conditions, the balance may differ (Oestmann et al., 2022; Petro et al., 2023; Li et al., 2024). Experiments that cross warming with water level and vegetation composition are needed to separate these direct and indirect pathways.

350 Nitrogen enrichment imposes a related pressure. In a well-drained temperate forest, experimental nitrogen addition reduced moss-mediated CH₄ uptake (Xu et al., 2026). In a temperate peatland, chronic nitrogen loading caused *Sphagnum* decline, promoted graminoid expansion, and weakened the ecosystem's cooling effect through altered greenhouse-gas exchange (Lu et al., 2025). Nitrogen deposition can thus affect the biofilter directly through moss and microbial physiology and indirectly by favoring aerenchymatous competitors.

355 The direction of the nitrogen response is scale-, dose-, and duration-dependent. In a short mesocosm experiment with nutrient-poor *Sphagnum*, nitrogen or phosphorus addition increased nutrient accumulation and reduced net CH₄ emission through enhanced oxidation without increasing moss growth (Kox et al., 2020). This short-term response does not contradict multi-year field inhibition; it indicates that initial nutrient relief, direct microbial effects, host stress, and eventual vegetation replacement occur on different time scales. Critical-load experiments should therefore follow both process rates
 360 and plant-community change across realistic deposition gradients instead of assigning one fixed nitrogen response to the biofilter.



5.3 Disturbance-driven transitions: permafrost thaw, succession, and seasonal dynamics

Rapid disturbance can move peatlands into transitional states in which CH₄ production and bypass transport increase faster than the moss oxidation layer develops. Permafrost thaw is a prominent example because it exposes previously frozen carbon, changes hydrology, and initiates ecological succession.

Young thermokarst bogs (~30 years since thaw) emitted approximately three times more CH₄ than mature bogs (~200 years), a difference associated with greater acetoclastic methanogenesis and early-successional hydrophilic vegetation (Heffernan et al., 2022). Over longer periods, succession toward *Sphagnum*-dominated conditions may reduce emission as substrate quality, vegetation, and surface oxidation capacity change, although trajectories vary among thaw features (Turetsky et al., 2020).

Submerged brown mosses show that filtering is not restricted to classic *Sphagnum* bogs. In Siberian polygonal ponds, *Scorpidium*-dominated communities oxidized 61–99% of sediment-produced CH₄ under diffusion-dominated conditions, whereas vascular-plant colonization provided a bypass (Knoblauch et al., 2015).

Seasonality remains a major source of uncertainty because many CH₄ budgets emphasize the growing season. Year-round isotope observations indicate continued oxidation near the peat–snow interface and a seasonal shift from plant-mediated transport in summer toward diffusion through peat and moss in winter (Li et al., 2025). Freeze–thaw periods contributed approximately 24% of annual CH₄ exchange in one boreal peatland (Miao et al., 2016). Global change may therefore alter annual emissions by redistributing both microbial activity and transport pathways across seasons.

Snow effects can persist beyond the winter measurement period. Experimental enhancement of soil frost reduced CH₄ emission during the following growing season, showing that winter conditions can modify later substrate supply, vegetation, or transport (Zhao et al., 2016). In contrast, laboratory winter warming altered carbon and nitrogen cycling but produced little CH₄ response in a moss-dominated peat mire (Miura et al., 2023). Snow depth or air temperature alone is therefore an incomplete predictor; annual studies should resolve peat thermal state, liquid-water availability, freeze-thaw pulses, vegetation damage, and carry-over effects on the subsequent growing season.

6 Restoring the moss biofilter: implications for peatland management and climate mitigation

Peatland restoration has traditionally emphasized raising water tables to suppress aerobic peat decomposition. The pathway framework developed here shows why hydrological recovery alone does not guarantee rapid CH₄ mitigation: rewetting can stimulate methanogenesis before a continuous, functional moss layer develops. Climate-effective restoration must therefore rebuild the oxidation interface while limiting aerenchymatous and ebullitive bypass. The evidence and principal design constraints for major restoration and paludiculture approaches are compared in Table 4.

6.1 Hydrological restoration is necessary but insufficient

Drainage reversal and water-table restoration are prerequisites for peat formation, but the immediate post-rewetting period can produce elevated CH₄ emissions when methanogenesis recovers more rapidly than moss-associated oxidation. The risk is



395 greatest where residual nutrients, labile carbon, inundated ditches, or aerenchymatous vegetation provide abundant substrate and efficient transport (Cooper et al., 2014; Strack et al., 2016).

Site history strongly conditions this response. Rewetting nutrient-rich agricultural peat without removing degraded topsoil can mobilize nutrients, promote eutrophication, and elevate greenhouse-gas emissions; topsoil removal can reduce these legacies and create more suitable conditions for *Sphagnum* establishment (Harpenslager et al., 2015). In a recent field
 400 comparison, removal of 5–30 cm of topsoil before *Sphagnum* revegetation converted treatment plots into net greenhouse-gas sinks, whereas plots without removal remained strong sources (Daun et al., 2026). The intervention, however, sacrifices peat volume and must be matched to site chemistry and restoration goals.

Restoration design should therefore begin from the site's hydrological, biogeochemical, and vegetation state. Where nutrient legacies and graminoid dominance persist, rewetting alone may establish a bypass-dominated system in which CH₄
 405 escapes through plant aerenchyma, open water, or ditches.

6.2 Rebuilding the moss oxidation layer can accelerate functional recovery

Because the living moss layer forms the interface for much of the observed CH₄ oxidation, its recovery is a logical restoration objective. Natural recolonization can be slow. The moss layer transfer technique (MLTT) seeks to accelerate establishment by moving donor moss material and its associated microbiome to degraded peat surfaces.

Evidence for MLTT is encouraging but context dependent. Short-term measurements show that the technique alters CO₂ and CH₄ efflux during early fen restoration (Lazcano et al., 2018), while revegetation of an industrially disturbed boreal
 410 peatland moved greenhouse-gas exchange toward recovery without immediately reproducing reference conditions (Engering et al., 2022). Independently, increasing *Sphagnum* abundance in restored cutover peatlands was strongly associated with recovery of methane-cycling microbial communities (Putkinen et al., 2018). These studies support active moss recovery but
 415 do not establish a universal timetable for net climate benefit.

MLTT performance depends on substrate and trophic status. On residual rich-fen peat, transferred bryophytes established poorly, whereas alternative rewetting increased vegetation cover and growing-season carbon uptake; persistent *Carex* dominance, however, was associated with higher CH₄ emission than at the reference fen (Turmel-Courchesne et al., 2023). Similarly, plant-functional-type experiments show that moss cover can enhance oxidation while graminoids increase
 420 ecosystem CH₄ release through vascular transport (Strack et al., 2017). Moss introduction should therefore be combined with hydrological and nutrient conditions that favor moss establishment without displacing the target fen community.

Evidence that active transfer accelerates climate recovery remains suggestive rather than conclusive. Most studies compare short-term gas exchange or vegetation trajectories, and improvements cannot always be separated from hydrological stabilization, substrate recalcitrance, or donor-site compatibility. Transferred microbial communities may
 425 establish before a continuous moss canopy forms, but their contribution to avoided ecosystem flux is rarely partitioned directly. Long-term tests should compare passive rewetting and active transfer using common baselines, include donor-harvest impacts, and follow both moss survival and pathway-specific CH₄ flux.



Restoration targets must also remain ecosystem specific. Promoting *Sphagnum* dominance is appropriate for degraded bogs but may be ecologically undesirable in naturally minerotrophic rich fens, where sedges and brown mosses are components of the reference community. A design optimized only to minimize CH₄ could displace characteristic vegetation or compromise biodiversity and water-quality objectives. Reference condition, conservation value, peat-forming function, and climate performance should therefore be specified as separate objectives before selecting moss transfer, nutrient removal, or vegetation control (Strack et al., 2017; Turmel-Courchesne et al., 2023).

6.3 Preventing bypass pathways determines long-term climate benefits

Long-term climate benefit depends on maintaining diffusion through an active oxidation layer and constraining pathways that bypass it. Three management principles follow from the evidence.

First, nutrient legacies must be addressed. Chronic nitrogen loading can suppress *Sphagnum* and favor graminoids, increasing the share of CH₄ transported through aerenchyma (Lu et al., 2025). Topsoil removal or other nutrient-management measures may be justified on heavily enriched sites, but their ecological costs and site specificity require explicit evaluation.

Second, restoration designs should minimize ditch and open-water hotspots. In *Sphagnum* paludiculture, production strips functioned as net greenhouse-gas sinks, whereas ditches were net sources and reduced the site-level benefit (Günther et al., 2017). In forestry-drained peatlands, moss-free ditches emitted 20.6 g CH₄ m⁻² yr⁻¹ compared with 2.6 g CH₄ m⁻² yr⁻¹ from moss-covered ditches (Rissanen et al., 2023). Ditch density, inundation pattern, and moss establishment must therefore be included in whole-site accounting.

Third, designs must remain robust under future drought, warming, and precipitation variability. Priority should be given to locally adapted moss communities, stable but not excessively inundated water levels, and spatial configurations that maintain continuous moss cover while limiting persistent open water.

Climate-oriented peatland restoration should consequently move beyond the generic objective of ‘rewetting peat’ toward reconstruction of a functional CH₄ oxidation layer within a favorable transport architecture. Combining hydrological recovery, site-appropriate moss establishment, nutrient management, and control of vascular and ebullitive bypass can reduce near-term CH₄ risk while supporting long-term peat-carbon accumulation.

These recommendations must be tested against the complete climate balance, not CH₄ alone. Rewetting can rapidly reduce aerobic peat CO₂ loss while increasing CH₄; topsoil removal can suppress nutrient-driven emissions but removes peat and requires handling; and paludiculture can create productive sinks on cultivation strips while infrastructure remains a source (Harpenslager et al., 2015; Günther et al., 2017; Darusman et al., 2023). Evaluation should therefore include CO₂, CH₄, N₂O, dissolved-carbon export, removed or harvested biomass, spatial hotspots, and off-site displacement across the whole intervention footprint. Reporting cumulative fluxes and more than one climate time horizon is especially important because the strong but short-lived forcing of CH₄ can dominate near-term outcomes even when long-term peat accumulation improves. Moss-associated oxidation is thus a valuable restoration mechanism, but not a sufficient climate-performance metric by itself.



7 Critical gaps and future research priorities

Although moss-associated CH₄ oxidation is increasingly recognized as a control on wetland greenhouse-gas exchange, its realized effect under global change remains difficult to predict. Biofilter performance is an emergent property of competition among diffusion through moss, vascular bypass, and episodic ebullition, not a fixed attribute conferred by moss presence. Research should therefore shift from reporting oxidation potential alone toward identifying and quantifying pathway dominance under field conditions.

7.1 Quantifying pathway partitioning across spatial and temporal scales

The most immediate priority is to quantify the relative contributions of diffusive, vascular, and ebullitive CH₄ transport under natural conditions. Few studies measure production, within-moss oxidation, plant-mediated transport, and bubble release concurrently. Without such partitioning, the fraction of total CH₄ flux intercepted by moss cannot be estimated reliably.

Stable-isotope tracers, pore-water CH₄ profiles, automated flux measurements, and molecular indicators of methanotrophic activity should be combined across microtopographic units and seasons. Pathway dominance can change through the year: vascular transport may dominate during active plant growth, whereas diffusion through peat and moss becomes relatively more important in winter (Li et al., 2025). Year-round pathway budgets are therefore essential for defensible wetland CH₄ inventories.

A minimum field design should pair total ecosystem exchange with independent constraints on each pathway. Automated transparent and dark chambers can resolve diurnal and episodic surface flux; plant enclosures or species-specific conductance measurements can constrain vascular transport; bubble traps or high-frequency chambers can capture ebullition; and depth-resolved concentration and $\delta^{13}\text{C}$ -CH₄ profiles can estimate oxidation. Moss moisture, temperature, O₂, thickness, species identity, vascular leaf area, and microform must be measured concurrently. Molecular data are most informative when linked to transcripts or isotope incorporation rather than used as stand-alone proxies. Applying this common design at restoration chronosequences and manipulation experiments would make cross-site synthesis substantially more defensible.

7.2 Identifying ecological thresholds and resilience under global change

A second priority is to identify the thresholds at which moss-filtered systems become bypass dominated. Moisture, temperature, nutrient status, and vegetation composition interact nonlinearly, and thresholds derived from single-factor experiments may not transfer across species or ecosystem types.

Hydrological thresholds are especially important: modest drying can expand the oxic zone, whereas severe drought damages moss tissues and the habitat required for oxidation (Daulat & Clymo, 1998; Keane et al., 2025a,b). Chronic nitrogen enrichment can similarly reduce moss-mediated CH₄ uptake and favor graminoid expansion (Lu et al., 2025; Xu et al., 2026). These responses imply hysteresis, because microbial recolonization may occur before the moss canopy and transport architecture recover.



Experiments should therefore test compound disturbances, such as warming with drought or nitrogen enrichment, and quantify both response thresholds and recovery trajectories. Identifying tipping points and hysteresis will improve prediction of when peatlands lose or regain their CH₄-buffering function.

Threshold terminology should be used operationally. A breakpoint in moss moisture, oxidation rate, or vegetation cover is not necessarily an ecosystem tipping point unless it produces a persistent state change with an alternative recovery path. Studies should predefine response variables for host viability, oxidation efficiency, pathway allocation, and net flux; impose replicated stress gradients; and continue observations after stress release. Comparing collapse and recovery trajectories would reveal true hysteresis, while repeated-measures models could distinguish abrupt transitions from steep but reversible responses.

7.3 Integrating the moss biofilter into ecosystem and Earth system models

A third priority is to represent moss-mediated oxidation explicitly in process-based models. Most wetland CH₄ models use water table, temperature, and vegetation type as aggregate controls, but do not resolve whether CH₄ reaches the atmosphere by diffusion, vascular transport, or ebullition.

The moss biofilter should be represented as a dynamic oxidation domain parameterized by moss biomass or thickness, moisture, O₂ supply, temperature, and diffusive CH₄ delivery. Vascular transport and ebullition require separate bypass terms because their flux is not fully exposed to this domain. The minimum process structure and corresponding state variables are summarized in Table 5.

A parsimonious mass balance can express atmospheric flux as the sum of (i) diffusive delivery multiplied by one minus moss-layer oxidation efficiency, (ii) vascular transport after any rhizosphere oxidation, and (iii) ebullition after any bubble dissolution or oxidation. The three transport fractions should be constrained to sum to one, while oxidation efficiency varies with moss state rather than being fixed by vegetation class. This structure exposes two distinct global-change sensitivities: drivers may alter the fraction routed through moss, the efficiency of oxidation within moss, or both. Parameter uncertainty should be propagated separately for pathway allocation and oxidation kinetics, then evaluated against year-round isotope and flux-partitioning observations.

Parameterization will require measurements that connect microbial function and plot-scale fluxes with landscape observations. Functional-gene abundance, stable-isotope constraints, chambers, eddy covariance, and remote sensing of vegetation structure and surface wetness can jointly support scaling. Existing remote-sensing approaches for peatland carbon exchange and pathway-explicit wetland CH₄ models provide a foundation, but their integration with moss-specific processes remains to be developed (Junttila et al., 2021; Nzotungicimpaye et al., 2021).

7.4 Expanding beyond boreal *Sphagnum* systems

Finally, the geographic and taxonomic generality of the moss biofilter remains unresolved. Most evidence comes from northern *Sphagnum*-dominated peatlands; tropical peatlands, Southern Hemisphere wetlands, rich fens, and non-*Sphagnum* bryophyte systems are sparsely represented.



Brown mosses and other bryophytes can support methane-oxidizing communities, but their oxidation capacity, host physiology, and environmental sensitivity may differ from those of *Sphagnum* (Liebner et al., 2011; Tveit et al., 2020). Coordinated studies across climatic regions and bryophyte lineages are needed to determine which elements of the pathway framework are general and which are biome specific.

The comparative unit should therefore be a host-pathway combination rather than 'moss' as one plant functional type. Submerged brown mosses can intercept diffusion through the water column, *Sphagnum* creates a capillary surface matrix, and feather-moss stands may contain active methanogens and emit CH₄ (Kanaparthi et al., 2017). Tropical systems may contain discontinuous bryophyte patches beneath vascular canopies, making local oxidation possible without a landscape-scale filter. Coordinated protocols spanning these functional settings would test whether hydration, O₂ supply, residence time, and bypass fraction provide transferable predictors despite taxonomic differences.

8 Conclusion

Bryophytes, particularly *Sphagnum*, can function as effective CH₄ biofilters by sustaining methanotrophs within a hydrated, oxygenated surface layer. Their climate effect is nevertheless contingent on transport: CH₄ must diffuse through the living moss layer rather than bypass it through vascular-plant aerenchyma or ebullition. Hydrology, light, warming, drought, nitrogen enrichment, vegetation change, permafrost thaw, and seasonality alter both oxidation capacity and pathway exposure. Consequently, moss cover alone is an inadequate predictor of ecosystem CH₄ flux. Restoration aimed at climate mitigation should rebuild a continuous moss oxidation layer, address nutrient and vegetation legacies, and minimize ditch, open-water, and vascular bypass, while evaluating full CO₂–CH₄ trade-offs. The framework also requires testing beyond northern *Sphagnum* peatlands and implementation in models that resolve diffusive, vascular, and ebullitive pathways separately. A pathway-explicit view should improve greenhouse-gas accounting and help identify where moss recovery is most likely to yield durable climate benefits.

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Code and data availability

No new observational data or scientific model code were generated for this review. The underlying measurements are available in the cited publications and their associated data resources. Sources and measurement bases for selected quantitative examples are identified in Tables 1–4. Search strings, evidence domains, the original screening account, and contextual additions are documented in the Supplement.



Author contribution

Conceptualization: DGK, HK; Data curation: DGK HK, JK; Investigation: DGK, HK, JK; Visualization: DGK, HK; Writing - original draft: DGK, HK, JK, GY and Writing - review & editing: DGK, HK, JK, GY

565 Data availability

The datasets analyzed in this review are derived from the published articles cited herein. All synthesized data are available within the tables and figures of this article.

Conflict of interest

570 There is no competing interest.

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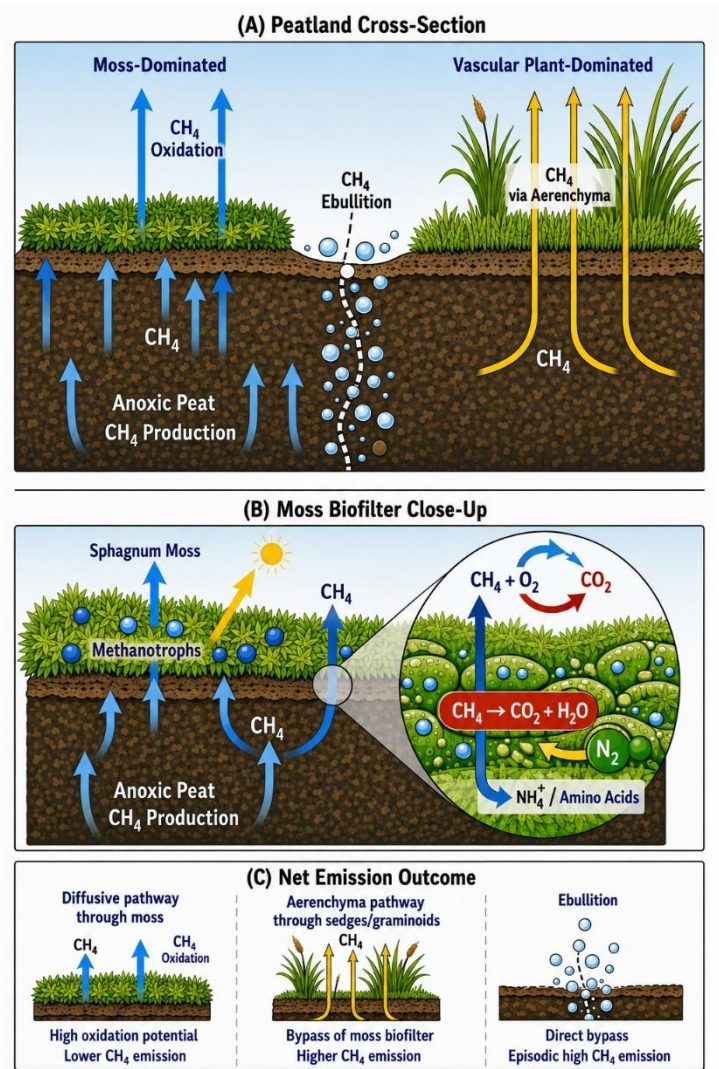
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Figure 1. Moss biofilter versus vascular shunt in peatlands. (A) Conceptual peatland cross-section showing CH₄ production in anoxic peat and contrasting transport pathways under moss-dominated and graminoid/sedge-dominated surfaces. Diffusive CH₄ moving through the moss layer can be oxidized by methanotrophs before emission, whereas aerenchyma-mediated plant transport and ebullition can bypass the moss-associated oxidation zone. (B) Close-up of the moss biofilter showing CH₄ oxidation by moss-associated methanotrophs, photosynthetic O₂ supply, CO₂ release and potential refixation, and possible N₂ fixation/N transfer. (C) Summary of net emission outcomes for diffusive transport through moss, aerenchyma-mediated transport, and ebullition. The figure is conceptual and not to scale.

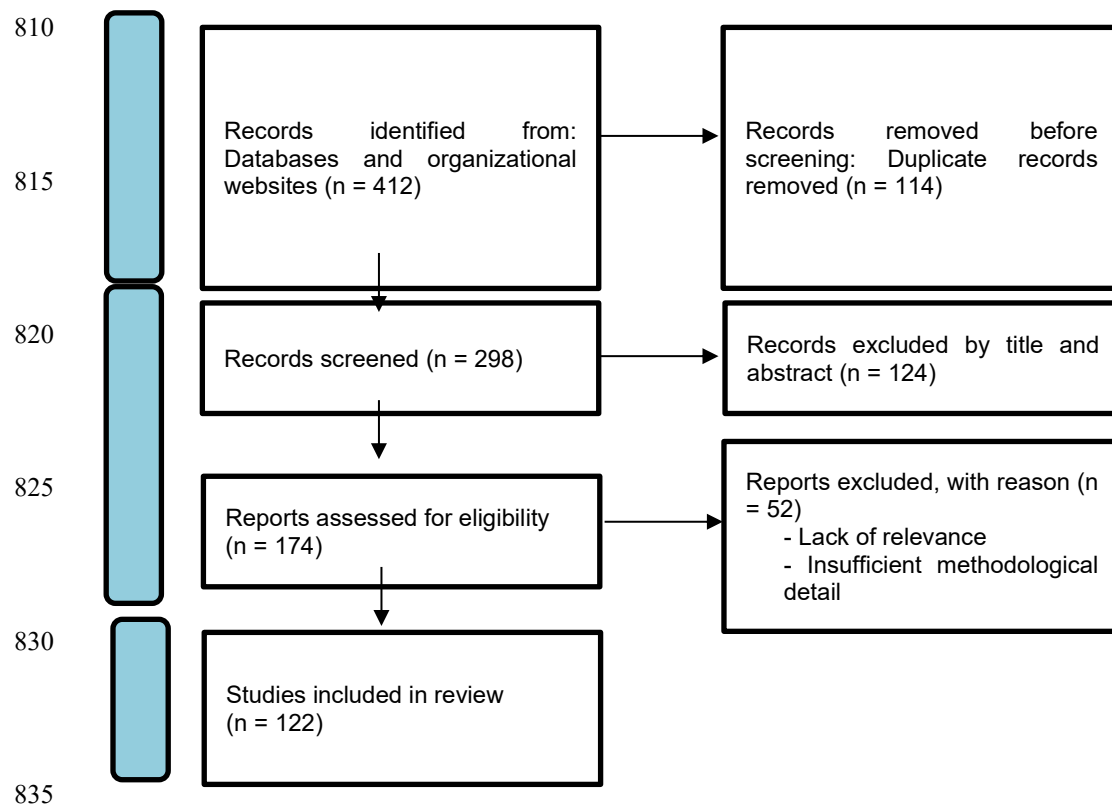
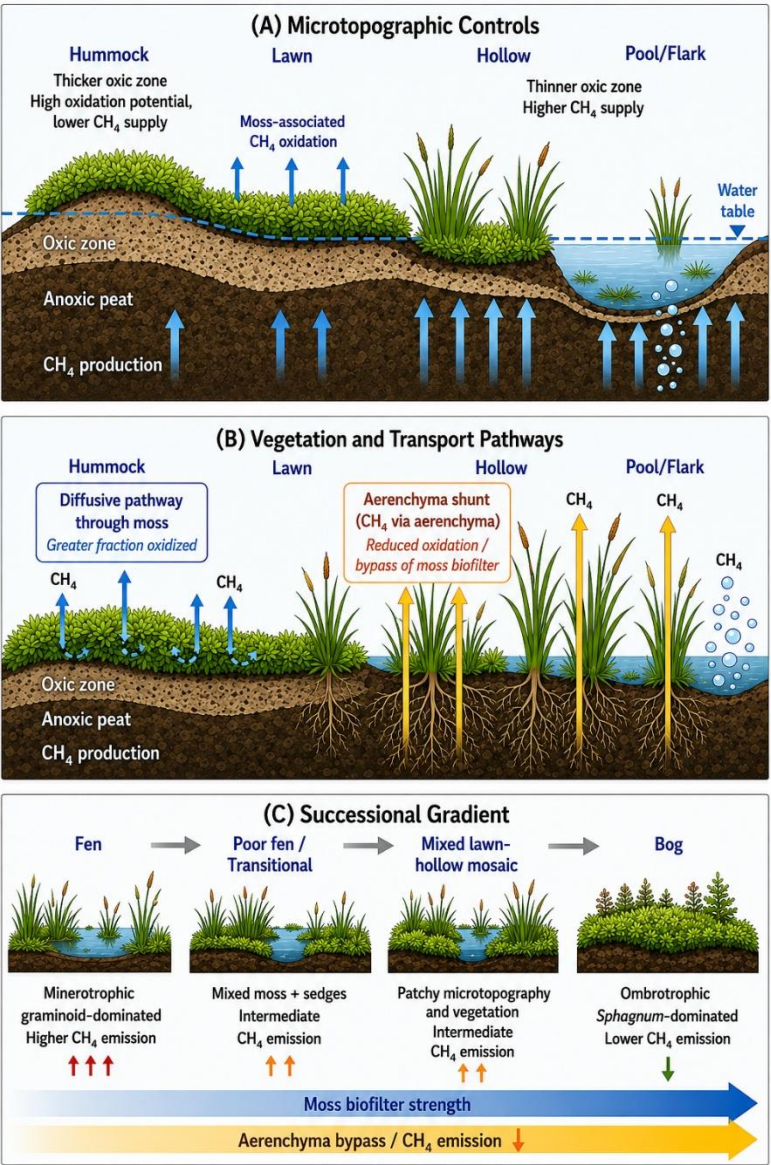


Figure 2. PRISMA flow diagram summarizing the article selection process.



840 **Figure 3. Ecological controls on moss-mediated CH₄ oxidation across peatland microforms and successional stages.** (A) Conceptual
microtopographic gradient showing how hummocks, lawns, hollows, and pools/flarks differ in water-table position, oxic-zone thickness,
CH₄ supply, and moss-associated oxidation potential. (B) Vegetation-pathway overlay illustrating that moss-dominated surfaces favor
diffusive CH₄ transport and oxidation, whereas graminoids and sedges promote aerenchyma-mediated bypass and pools/flarks can release
CH₄ by ebullition. (C) Successional gradient from minerotrophic, graminoid-dominated fen conditions toward ombrotrophic, Sphagnum-
845 dominated bog conditions, with increasing moss biofilter strength and generally decreasing CH₄ emission. The figure is conceptual and not
to scale.



Table 1. Mechanistic pathways underlying moss-associated CH₄ mitigation and qualitative confidence based on the evidence hierarchy in Section 3.

Mechanism	How it can lower net CH ₄ emissions	Representative evidence	Evidence confidence and basis
Moss provides a hydrated habitat for aerobic methanotrophs	Maintains an oxygenated niche close to diffusive CH ₄ supply, increasing oxidation before emission.	Submerged <i>Sphagnum</i> supported abundant CH ₄ oxidizers and reduced mesocosm CH ₄ emission by 93% (Kox et al., 2021).	Moderate to high: manipulative, molecular, and microenvironmental evidence; ecosystem-scale effectiveness remains pathway dependent.
Photosynthetic O ₂ supply stimulates CH ₄ oxidation	Increases local O ₂ availability and can shift submerged systems from net CH ₄ emission toward uptake.	Light increased CH ₄ oxidation approximately fivefold in <i>Sphagnum</i> (Kox et al., 2020); daylight shifted brown-moss ponds toward net uptake (Liebner et al., 2011).	High but context dependent: supported by manipulative and field evidence; responses depend on CH ₄ supply, hydration, and experimental conditions.
Methanotrophs recycle CH ₄ -derived carbon and may contribute fixed nitrogen	Returns oxidation-derived CO ₂ or microbial carbon to moss tissues; diazotrophic methanotrophs can supplement nitrogen supply.	¹³ C-CH ₄ labeling traced methane-derived carbon into microbial biomarkers and moss sterols (Liebner et al., 2011); methanotrophy stimulated nitrogen fixation during peatland development (Larmola et al., 2014).	High for carbon transfer; moderate and context dependent for nitrogen transfer.
Water-mediated recolonization restores methanotroph function after disturbance	Provides functional insurance after drying or disturbance when the moss host remains viable.	Bathing moss in non-sterile flark water rapidly restored colonization and strongly increased <i>pmoA</i> abundance (Putkinen et al., 2012).	Moderate: supported by transplantation and molecular evidence; long-term recovery depends on moss survival.
Species and microhabitat regulate within-moss oxidation	Determine CH ₄ supply, O ₂ status, hydration, and the spatial overlap required for methanotrophy.	Oxidation potential was high in pool <i>Sphagnum</i> and low in hummock or lawn moss, tracking in situ CH ₄ supply (Kip et al., 2012).	Moderate: supported by rate measurements and microhabitat contrasts, but potential activity and realized ecosystem flux can diverge.
Vegetation structure controls vascular bypass	Aerenchymatous plants transport CH ₄ around the moss oxidation zone, reducing the fraction accessible to methanotrophs.	Moss layers oxidized 61–99% of sediment-produced CH ₄ in diffusion-dominated ponds lacking vascular plants; exposure declined after vascular-plant colonization (Knoblauch et al., 2015).	High for the bypass mechanism; context dependent for net ecosystem flux.
Winter conditions can preserve diffusive exposure	Snow insulation can maintain unfrozen, moist microsites in which CH ₄ remains accessible to oxidation outside the growing season.	Year-round δ ¹³ C-CH ₄ measurements indicated oxidation near the peat–snow interface (Li et al., 2025); freeze–thaw periods contributed materially to annual exchange (Miao et al., 2016).	Emerging: isotopic and seasonal-flux evidence is available, but direct winter process measurements remain limited.
Ebullition bypasses the moss oxidation zone	Rapid bubble release shortens residence time in the oxygenated moss layer and limits oxidation during episodic events.	Ebullitive losses contributed to emissions from horticultural peatlands, and infilled ditches acted as CH ₄ hotspots after rewetting (Bieniada & Strack, 2021; Cooper et al., 2014).	Emerging and context dependent: ebullition is well established, but its partitioning by moss cover and microtopography is poorly constrained.



Table 2. Representative moss-mediated CH₄ uptake and oxidation rates across contrasting ecosystems.

System and host	Measurement basis	Reported value	Interpretation and source
Well-drained temperate forest; mixed moss understory	Moss-associated difference in area-based methane uptake	0.77 kg CH ₄ -C ha ⁻¹ yr ⁻¹ under control conditions	A moss-removal comparison estimates a net moss-associated contribution, not oxidation by a defined methanotroph population. This upland example is contextual evidence and is not a peatland biofilter rate (Xu et al., 2026).
Patagonian peatland pools; <i>Sphagnum magellanicum</i>	Moss-mass-normalized oxidation potential	23 μmol CH ₄ g ⁻¹ dry mass d ⁻¹	Potential rate under the reported assay conditions. Area-based field attenuation requires moss biomass, methane delivery, and pathway information (Kip et al., 2012).
Arctic polygonal ponds; submerged brown moss	Fraction of sediment-produced methane oxidized	61–99 %	Study-specific estimates for diffusion-dominated ponds without vascular plants. The denominator is sediment production, not atmospheric methane uptake or a generic wetland emission baseline (Knoblauch et al., 2015).
Siberian polygonal ponds; submerged brown moss	Net daytime exchange at the pond surface	Uptake of 1.7 mg CH ₄ m ⁻² d ⁻¹	Net exchange integrates production, oxidation, transport, and storage. A light-period observation cannot establish an annual sink or a universal moss oxidation rate (Liebner et al., 2011).



Table 3. Major environmental controls on moss-mediated CH₄ oxidation and biofilter persistence.

Driver	Mechanism	Biofilter response	Quantitative evidence	Threshold or critical condition	Citations
Hydrology (water-table depth)	Controls the anoxic production zone, O ₂ penetration, gas diffusion, and moss hydration.	Nonlinear: modest drawdown can increase oxidation, whereas severe desiccation impairs the host and microbial habitat.	CH ₄ efflux generally declined as the oxic zone expanded; effects varied with vegetation and microsite.	Irreversible damage below approximately 12 g g ⁻¹ water content in <i>S. palustre</i> and 18 g g ⁻¹ in <i>S. squarrosum</i> .	Daulat & Clymo (1998); Riutta et al. (2020); Keane et al. (2025a,b)
Light (PAR) ¹	Photosynthesis by chlorophyllous moss tissues supplies O ₂ to associated methanotrophs.	Usually stimulates oxidation when CH ₄ supply and hydration are adequate.	Illumination increased oxidation ~5-fold and nitrogen fixation ~3-fold; brown-moss ponds shifted from daytime uptake (−1.7 mg CH ₄ m ⁻² d ⁻¹) to dark emission (+21.6 mg CH ₄ m ⁻² d ⁻¹).	No general light threshold has been established; the response depends on photosynthesis and substrate supply.	Kox et al. (2020); Liebner et al. (2011)
Temperature	Changes methanogenesis, methanotrophy, host physiology, hydrology, and vegetation composition.	Context dependent; pathway composition modifies net temperature sensitivity.	Emission Q ₁₀ ² averaged 1.71 in moss-dominated wetlands and 2.26 in vascular-plant-dominated wetlands.	Whole-ecosystem warming of up to +9°C decoupled nitrogen fixation from CH ₄ oxidation and was associated with severe <i>Sphagnum</i> mortality.	Li et al. (2024); Zhang et al. (2021); Oestmann et al. (2022); Petro et al. (2023)
Nitrogen enrichment	Alters moss and methanotroph physiology and can favor aerenchymatous graminoids.	Chronic loading can weaken direct uptake and shift vegetation toward vascular bypass.	Control moss-mediated uptake was 0.77 kg C–CH ₄ ha ⁻¹ yr ⁻¹ and declined under nitrogen addition; long-term peatland enrichment caused <i>Sphagnum</i> mortality and graminoid expansion.	No transferable critical load is established; risk rises when moss cover is lost to graminoids.	Xu et al. (2026); Lu et al. (2025)
Drought and desiccation	Impairs moss photosynthesis and structure; disrupts the hydrated habitat and O ₂ supply.	Potentially reversible after moderate drying but persistent after host damage.	Water-mediated dispersal can rapidly restore methanotroph colonization after rewetting.	Species-specific moss-moisture thresholds determine host survival and recovery.	Putkinen et al. (2012); Keane et al. (2025a,b)
Snow and freeze–thaw	Snow insulates the peat–moss interface; freezing alters gas transport and substrate release.	Winter oxidation persists, but episodic release can remain important to annual budgets.	Isotopes indicate oxidation near the peat–snow interface; freeze–thaw periods contributed ~24% of annual CH ₄ exchange in one boreal peatland.	Controlled by snow insulation, peat temperature, ice structure, and seasonal transport pathways.	Li et al. (2025); Miao et al. (2016)



Driver	Mechanism	Biofilter response	Quantitative evidence	Threshold or critical condition	Citations
Permafrost thaw and thermokarst	Exposes frozen carbon, changes hydrology, and initiates vegetation succession.	Early high-emission phase may weaken as <i>Sphagnum</i> and surface oxidation develop.	Young thermokarst bogs (~30 yr) emitted about three times more CH ₄ than mature bogs (~200 yr); submerged brown mosses oxidized 61–99% under diffusion-dominated conditions.	Trajectory depends on thaw feature, hydrology, substrate, and the balance between graminoids and mosses.	Heffernan et al. (2022); Knoblauch et al. (2015); Liebner et al. (2011); Turetsky et al. (2020)

¹ PAR = photosynthetically active radiation.

² Q₁₀ = fold change in rate per 10°C increase in temperature.

³ Young and mature thermokarst bogs denote approximately 30 and 200 years since thaw initiation, respectively.

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Table 4. Restoration and paludiculture interventions, methane outcomes, and principal design constraints.

Intervention	Approach	Early CH ₄ outcome (0–3 yr)	Outcome at 3–10 yr	GHG implication	Co-benefits and trade-offs	Success factors	Sources
Passive rewetting (ditch blocking)	Raise the water table and allow natural recolonization.	CH ₄ can increase where labile carbon, sedges, inundated surfaces, or infilled ditches become hotspots.	Flux may decline as vegetation and moss cover reorganize, but trajectories are site specific.	CO ₂ losses usually decline rapidly; recovery of a net carbon sink may require ~6–10 yr and does not guarantee low CH ₄ .	Low intervention cost and hydrological recovery, but risk of persistent graminoid or open-water hotspots.	Stable hydrology, limited nutrient legacy, and establishment of appropriate peat-forming vegetation.	Cooper et al. (2014); Strack et al. (2016); Waddington et al. (2010)
Moss layer transfer technique (MLTT)	Transfer donor moss fragments and associated microbiota to prepared peat surfaces.	Can accelerate moss establishment; early CH ₄ and CO ₂ exchange may remain distinct from reference conditions.	Recovery depends on substrate, hydrology, trophic status, and competition with vascular plants.	Potential to improve the restoration trajectory; no universal time to net climate benefit is established.	Transfers a peat-forming community but requires donor material and can fail on unsuitable rich-fen substrates.	Surface preparation, hydrological stability, compatible donor material, and control of competitive graminoids.	Lazcano et al. (2018); Engering et al. (2022); Turmel-Courchesne et al. (2023)
Topsoil removal plus rewetting	Remove nutrient-rich degraded topsoil (5–30 cm) before rewetting and <i>Sphagnum</i> establishment.	Can strongly suppress nutrient mobilization and CH ₄ emissions relative to retaining enriched topsoil.	Field treatments remained net sinks where revegetation and hydrology were successful.	Removal treatments yielded –4.5 to –5.7 t CO ₂ -eq ha ^{–1} yr ^{–1} , versus +43.7 t CO ₂ -eq ha ^{–1} yr ^{–1} without removal in one study.	Reduces labile carbon and nutrient legacies but removes peat and increases cost and disturbance.	Site-specific removal depth, stable water table, and rapid revegetation.	Harpenslager et al. (2015); Daun et al. (2026)
<i>Sphagnum</i> farming (paludiculture)	Cultivate <i>Sphagnum</i> biomass on rewetted peat for horticultural use.	Production strips can be net sinks, whereas ditches and open water can dominate CH ₄ emissions.	Sink potential depends on hydrological control; warming and surface drying can increase greenhouse-gas losses.	Production strips showed net balances of approximately –5 to –9 t CO ₂ -eq ha ^{–1} yr ^{–1} , while ditches were net sources in one site.	Renewable biomass production and an alternative to drainage, offset by infrastructure and whole-site hotspot risks.	Minimize ditch area, manage irrigation, address topsoil legacies, and select locally suitable mosses.	Günther et al. (2017); Rissanen et al. (2023); Oestmann et al. (2022)



Intervention	Approach	Early CH ₄ outcome (0–3 yr)	Outcome at 3–10 yr	GHG implication	Co-benefits and trade-offs	Success factors	Sources
Topsoil retention plus rewetting	Rewet agricultural peat without removing nutrient-rich topsoil.	May produce CH ₄ and nutrient pulses, eutrophication, and graminoid expansion.	Persistent source conditions are possible where labile substrates and bypass vegetation remain.	A strong net source (+43.7 t CO ₂ -eq ha ⁻¹ yr ⁻¹) occurred in the no-removal treatment of one field study.	Restores water level with less excavation but retains nutrient and substrate legacies.	Use only after site assessment; pair with nutrient and vegetation management where removal is infeasible.	Harpenslager et al. (2015); Daun et al. (2026)
MLTT in rich fens	Apply transferred mosses to minerotrophic, nutrient-rich residual peat.	Bryophyte establishment can be poor and Carex-associated CH ₄ emission can remain high.	Outcomes depend on hydrological connectivity and whether target fen vegetation establishes.	Site specific; growing-season carbon uptake can recover without reproducing the reference CH ₄ balance.	May support fen biodiversity, but a bog-oriented moss target can be ecologically inappropriate.	Match donor material and method to fen chemistry; avoid suppressing desired fen vegetation solely to reduce CH ₄ .	Strack et al. (2017); Turmel-Courchesne et al. (2023)
Reversal of peatland forestry drainage	Rewet drained forest peat and manage ditch and field vegetation.	Ditches can remain major CH ₄ sources; moss cover markedly lowers ditch-scale emission.	Sink recovery is possible as hydrology and moss cover stabilize, but requires whole-site verification.	Moss-free ditches emitted 20.6 versus 2.6 g CH ₄ m ⁻² yr ⁻¹ from moss-covered ditches in one study.	Supports biodiversity and water quality but ends timber production and can create wet hotspots.	Block or reprofile ditches, establish moss in ditch networks, and maintain long-term hydrological control.	Rissanen et al. (2023)

¹ MLTT = moss layer transfer technique.

² Net greenhouse-gas balance is expressed as t CO₂-eq ha⁻¹ yr⁻¹; negative values denote a net sink and positive values a net source.

³ Quantitative outcomes are study specific and should not be interpreted as universal performance ranges.

⁴ DOC = dissolved organic carbon.



Table 5. Proposed representation and evaluation of moss-associated methane oxidation in process models. These are candidate components to audit and test, not validated parameter values or claims that existing models omit these processes.

Component	Candidate representation	Evaluation requirement
Control volume and methane balance	Production, lateral exchange, storage change, oxidation sinks, and atmospheric release defined for the same spatial domain and time step.	Test closure of the methane balance, including winter storage and episodic release.
Moss-associated oxidation	A distinct oxidation domain linked to living moss, hydration, methane delivery, oxygen supply, and temperature.	Separate moss oxidation from aerobic peat and rhizosphere oxidation; evaluate against process measurements.
Diffusive delivery	Methane supply and residence time derived from concentrations, transport properties, and hydrological state.	Constrain delivery separately from oxidation capacity; avoid treating laboratory potential as a field rate.
Vascular transport	Species-dependent transport linked to plant traits, phenology, and access to methane, retaining rhizosphere effects.	Use pathway measurements and production constraints; vegetation cover alone is an incomplete proxy.
Ebullition and pathway transfers	Gas storage, bubble release, dissolution, and any subsequent oxidation represented without double counting.	Resolve event frequency and magnitude with observations of bubbles, dissolved gases, and total flux.
Allocation and recovery	Pathway fractions partition one common transport quantity; moss recovery and microbial activity can have different time scales.	Propagate allocation and oxidation uncertainty separately. Add threshold or hysteresis functions only when supported by suitable observations.