



Review

Impact of climate change-induced alterations in peatland vegetation phenology and composition on carbon balance



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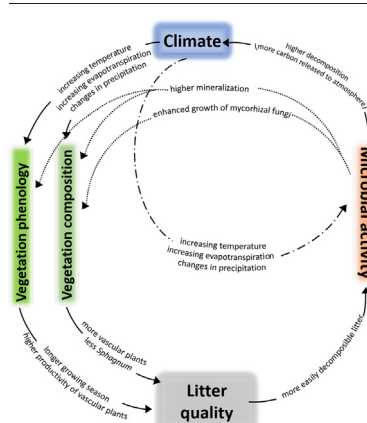
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HIGHLIGHTS

- Climate change induces changes in peatland vegetation phenology and composition.
- Shrubs produce more flowers and phenophases of vascular plants start sooner.
- Peat mosses are becoming less abundant and vascular plants cover is increasing.
- Changing peatland vegetation modifies the carbon balance.

GRAPHICAL ABSTRACT



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ABSTRACT

Global climate is changing faster than humankind has ever experienced. Model-based predictions of future climate are becoming more complex and precise, but they still lack crucial information about the reaction of some important ecosystems, such as peatlands. Peatlands belong to one of the largest carbon stores on the Earth. They are mostly distributed in high latitudes, where the temperature rises faster than in the other parts of the planet. Warmer climate and changes in precipitation patterns cause changes in the composition and phenology of peatland vegetation. Peat mosses are becoming less abundant, vascular plants cover is increasing, and the vegetation season and phenophases of vascular plants start sooner. The alterations in vegetation cause changes in the carbon assimilation and release of greenhouse gases. Therefore, this article reviews the impact of climate change-induced alterations in peatland vegetation phenology and composition on future climate and the uncertainties that need to be addressed for more accurate climate prediction.

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1. Introduction

The latest report of the Intergovernmental Panel on Climate Change (IPCC) reported that the climate is changing faster than expected (IPCC, 2021). Every decade is warmer than the previous one, and temperature over land has already increased by 1.5 °C compared to the preindustrial era. The changes in global climate are undoubtedly caused by anthropogenic activities and impact a plethora of processes on Earth. The temperature will certainly continue to increase in the next decades, and extreme weather events, such as hot and drought waves and extreme precipitation events, will become more frequent (IPCC, 2021). The impact of climate change at high latitudes and altitudes is projected to be more pronounced than in other regions of the globe (Hoegh-Guldberg et al., 2018; IPCC, 2021). These regions are typical for boreal forests, tundra, and peatlands, all of which are undergoing and will experience dramatic changes due to global warming (Bjorkman et al., 2018; Boulanger et al., 2017; Dise, 2009).

Northern peatlands belong to the most important ecosystems of the Earth. Despite the fact that peatlands cover only around 3% of the terrestrial surface or 1% of the total Earth surface, they are the ecosystem with one of the highest concentrations of stored carbon. It is estimated that about 30% of all carbon stored in the world's soils is stored in peatlands (Gorham, 1991). The high carbon accumulation potential of peatlands is due to very specific conditions, namely low pH, low nutrient and oxygen availability created by waterlogged conditions, and specific vegetation of the peatlands (van Breemen, 1995). Due to their high water holding capacity, specific morphology and physiology, and chemical composition, *Sphagnum* spp. are able to modify the environment in their favor and create adverse conditions for most of the vascular plants; thus, the *Sphagnum* spp. are considered as ecosystem engineers (Malmer et al., 2003; Rochefort, 2000; van Breemen, 1995). Only very specific vascular plants are able to co-inhabit the peatlands along with mosses (Chapin et al., 1996; Turetsky et al., 2012). The peatland's functions and peat accumulation rate depend on the physiological status and photosynthetic activity of plants and on proportions of plant functional groups in the vegetation cover (Kuiper et al., 2014; Mao et al., 2018).

Generally, plants growing in the peatlands can be divided into five plant functional groups: a) mosses, b) graminoids – grasses (Poaceae), sedges (Cyperaceae) and rushes (Juncaceae), c) forbs – annual broadleaf herbs and pteridophytes, d) shrubs – subdivided to evergreen and deciduous, and e) trees (Moore et al., 2002; Rupp et al., 2019; Walker et al., 2015). Denser cover of the taller shrubs and trees in peatlands are normally prevented by high water saturation and low nutrient availability, and if it occurs, it is a sign of climate change (Holmgren et al., 2015). Most of the peatlands are covered by mosses, graminoids, and creeping or low shrubs (Wiedermann et al., 2017).

Mosses and especially *Sphagnum* spp. play a crucial role in peatlands' carbon accumulation (Buttler et al., 2015). They belong to evolutionary primitive plants without roots, conducting tissues, or cuticula protecting

their surface from water loss (Chiapusio et al., 2021). Peat mosses acquire nutrients through the whole surface, mostly from atmospheric deposition, and water supply to the physiologically active part is provided by precipitation and capillary action (Hájek and Beckett, 2008; Hyryläinen et al., 2018; Weston et al., 2015). Unlike the majority of vascular plants, *Sphagnum* spp. growth continues as long as the mosses are not frozen (Malmer et al., 2003).

Graminoids growing in waterlogged conditions of peatlands must have a root system adapted to low oxygen conditions. Their roots contain aerenchyma, the sponge-like tissue with air channels, which allows proper aeration of root tissues, but also gas exchange between the atmosphere and peat (Noyce et al., 2014; Visser et al., 2000). The foliage of graminoids dies in the autumn and typically stays in the canopy for at least one year (Chapin et al., 1996). Plants mostly overwinter as rhizomes, and new leaves appear in spring when the temperature is suitable (Bernard and Hankinson, 1979; Wein, 1973).

Peatland shrubs had to evolve different strategies to cope with the continuous growth of mosses, which would otherwise overgrow and deprive them of light. Their shoots need to either constantly grow, or new shoots must develop from buds of subterranean runners. Roots of shrubs are mostly shallow, and adventitious roots are formed once the shoot gets overgrown by mosses (Buttler et al., 2015; Malmer et al., 1994). Mycorrhizal fungi help shrubs with shallow roots with nutrient acquisition and also water supply (Cullings, 1996). Leaf of many evergreen shrubs found in peatlands have traits connected with lowering water losses, such as a thick layer of waxes, stomata only on the abaxial side, or revolute margins (Buttler et al., 2015). Deciduous shrubs usually have thinner leaves and a shorter photosynthetically active season because, unlike evergreen shrubs, they first need to develop leaves at the beginning of the vegetation season (Chapin et al., 1996).

Many different plant communities may exist in the same peatland (Bandopadhyay et al., 2021), but based on the hydrology, nutrient availability, pH, calcium content, and vegetation composition, peatlands are divided into two major groups: bogs and fens (Hájek et al., 2006). Bogs are the type of peatlands where the surface is due to accumulated peat so high above the groundwater level that it does not receive any minerogenic water. The water regime of bogs and the plant water supply depends on atmospheric precipitation, evapotranspiration, and water holding capacity (Aaby, 1976; Mauquoy et al., 2002b). The vegetation of bogs is dominated by *Sphagnum* spp. and shrubs with the lower cover of graminoids, forbs, and trees (Hájek et al., 2006). On the other hand, fens are fed with water and nutrients from ground or surface water, along with precipitation. This causes higher basic cations content and higher pH. Fens are generally dominated by *Sphagnum* spp. and graminoids with the considerable cover of forbs and lower abundance of shrubs and trees (Hájek et al., 2006; Weltzin et al., 2003).

The majority of today's peatlands started to form between 8 and 6 thousand years ago, and there are hardly peatlands older than twenty thousand

years (Gorham et al., 2007). The current rate of climate change is fastest than in the last twenty million years, implicating that the ongoing climate change is faster than existing peatlands have ever experienced (Tripathi et al., 2009). The information regarding the peatland is still limited; thus, the peatlands are still not fully included in climate models, which brings uncertainties to predictions about future climate (IPCC, 2021). Therefore, the objectives of this review are to (1) summarize the existing knowledge about the impact of climate change on peatland vegetation phenology and composition, (2) improve the understanding of impact of these changes on carbon balance and 3) provide a future direction to peatland research for the purpose to understand the basic mechanism of peatland vegetation interaction with climate.

2. Changes in peatland vegetation phenology

Changes in plant phenology are one of the consequences of climate change; therefore, a shift in plant phenology may be considered an indicator of the changing climate and the adaptation of species to new environmental conditions (Parmesan and Yohe, 2003; Visser and Both, 2005). The intensity of change in plant life cycle varies for different species, but the general trend is an earlier onset of phenophases observed in the warmer and still warming world (Menzel et al., 2006; Peñuelas and Filella, 2001). This is caused by the fact that temperature is one of the most important factors controlling the plant's developmental process (Hatfield and Prueger, 2015). However, the warming at high latitudes is not connected just with the positive effect of higher temperatures on plant development. The higher occurrence of extremely warm periods during winter causes snow to thaw and exposes the plants' flower buds to freezing temperatures during the night or subsequent low-temperature period, which causes the delay and reduction of fruit production (Bokhorst et al., 2008; Callaghan et al., 2004). Bryophytes exposed to freezing temperatures without snow cover

suffer from stress which then negatively impacts the beginning of the vegetation season (Küttim et al., 2019). In some regions, climate warming causes less frost days in a year, but increases their number during the growing season. That increases the days in a season plants are exposed to freezing temperature (Liu et al., 2018). Despite the effect of changing climate on plants is not only straightforward, it is clear that changes in plant phenology caused due to environmental factors will have a wide range of consequences for the ecosystem, agriculture, forestry, world economy, and human health (Peñuelas et al., 2002). Therefore, there is a need for close examination of the impact of global warming on the ecosystems to predict at least the reaction of dominant species and either prepare for the changes or take measures to avoid the changes, which may be destructive to the whole ecosystem.

Several experiments studying the phenological response of peatland vegetation to different climate change scenarios have been performed (Table 1). Flowering is one of the most important stages in a plant's life as the next generation of the species depends on it. Therefore, plants evolved various mechanisms to control the time of flowering and the number of flowers produced (Gaudinier and Blackman, 2020). Ambient temperature is one of the most important factors regulating flowering (Cho et al., 2017). A study on peatland shrubs *Andromeda polifolia* and *Rubus chamaemorus* has revealed that increased temperature in various seasons impacts the flowering to a different extent. While warmer summer or winter do not alter the number of produced flowers, the total number of flowers increases when spring temperature was significantly higher than average (Aerts et al., 2004). Based on current predictions of changes in climate, the flower production of these shrubs will very likely increase in the next decades (IPCC, 2021). However, an increased number of flowers accompanied by higher production of fruits does not necessarily mean a better chance for generative reproduction, especially in the case of *Rubus chamaemorus*, which is also known as cloudberry. The fruits are harvested

Table 1
Changes in the phenology of peatland inhabiting plants caused by climate change.

Climate factor (change)	Time period	The method used for manipulation	Observation related to phenology		References	
			Parameter	Change		
Temperature (increase)	Spring of two years	Open-top chambers	Total flower production of <i>Andromeda polifolia</i>	+	(Aerts et al., 2004)	
			Total flower production of <i>Rubus chamaemorus</i>	+		
			Median flowering date of <i>Andromeda polifolia</i>	-		
			Median flowering date of <i>Rubus chamaemorus</i>	-		
Temperature (increase)	Summer of two years	Open-top chambers	Total flower production of <i>Andromeda polifolia</i>	0	(Aerts et al., 2004)	
			Total flower production of <i>Rubus chamaemorus</i>	0		
			Median flowering date of <i>Andromeda polifolia</i>	-		
			Median flowering date of <i>Rubus chamaemorus</i>	0		
Temperature (increase)	Winter of two years	Snow addition	Total flower production of <i>Andromeda polifolia</i>	0	(Aerts et al., 2004)	
			Total flower production of <i>Rubus chamaemorus</i>	0		
			Median flowering date of <i>Andromeda polifolia</i>	-		
			Median flowering date of <i>Rubus chamaemorus</i>	-		
Temperature (increase)	Fourth and fifth seasons after the beginning of the manipulation	Open-top chambers	Timing of total maximum leaf area of forbs in the southern fen (62°N)	+	(Mäkiranta et al., 2018)	
			Timing of total maximum leaf area of forbs in the northern fen (68°N)	+		
			Timing of total maximum leaf area of shrubs and sedges in the southern (62°N) and northern (68°N) fens	0		
			The length of growing period of forbs in the southern fen (62°N)	+		
			The length of growing period of forbs in the northern fen (68°N) and shrubs and sedges in the southern (62°N) and northern (68°N) fens	0		
Temperature (increase)	Second season after the beginning of the manipulation	Open-top chambers	Length of female and male spikes of <i>Carex bigelowii</i>	+	(Stenström and Jónsdóttir, 1997)	
			Flowering time of <i>Carex bigelowii</i>	0		
			Prefloration period of <i>Carex bigelowii</i>	-		
	Second to the fifth season after the beginning of the manipulation		Beginning and end of stigma receptivity to the pollen of <i>Carex bigelowii</i>	-		(Stenström and Jónsdóttir, 1997, 2004)
			Beginning and end of pollen release of <i>Carex bigelowii</i>	-		
			Gender phase overlap of <i>Carex bigelowii</i>	+		
Temperature (increase)	Three seasons	Open-top chambers	Time of maximal leaf biomass occurrence of <i>Eriophorum vaginatum</i>	-	(Sullivan and Welker, 2005)	
	Second season		Beginning of root growth of <i>Eriophorum vaginatum</i>	-		
Water table level (decrease)	Fourth and fifth seasons after the beginning of the manipulation	A ditch dug around the plot	Timing of total maximum leaf area of forbs, shrubs, and sedges in the southern (62°N) and northern (68°N) fens	0	(Mäkiranta et al., 2018)	
			The length of growing period of sedges in the southern (62°N) and northern (68°N) fens	+		
			The length of growing period of forbs and shrubs in the southern (62°N) and northern (68°N) fens	0		

Change: no change 0, decrease (sooner) -, increase (later) +.

by people and eaten by birds. Therefore, people and animals may benefit from higher fruit production more than the plant itself, which shows how complex the relationships in nature are (Leiřová-Svobodová et al., 2018). The impact of climatic conditions on flowering is also very intricate as many species create the flower buds in the previous year, and the environmental conditions of the present year influence flowering in the following year more than the flowering of the observed year (Lyngstad et al., 2017).

Not only the number of flowers is an important variable, but also the time of flowering, which is generally more dependent on the ambient temperature (Cho et al., 2017). *Andromeda polifolia* and *Rubus chamaemorus* bloom sooner when winter and spring are warmer. Higher summer temperature promotes the beginning of *Andromeda polifolia* flowering (Aerts et al., 2004). Unlike shrubs, the emergence of sedge *Carex bigelowii* flowers is not changed by increased temperature. However, once the flowers appear, pollen release and stigma receptivity start faster in warmer conditions (Stenström and Jónsdóttir, 1997, 2004). Earlier stigma receptivity and pollen release result in earlier pollination and grain establishment, which positively affect the grain weight and possibly viability of grains. Hence, the warmer conditions may increase the chance of healthy progeny establishment and spread of the species (Stenström, 1999). Despite *Carex bigelowii* being, to some extent, self-pollinated, cross-pollination is the dominant pollination strategy of species. Therefore, the prolonged gender phase overlap resulting from increased temperature will not have any significant impact on grain viability (Stenström et al., 2001; Stenström and Jónsdóttir, 2004). Although the flowering is an essential phenophase for generative reproduction, studies of flowering responses of peatland plants are just one piece in the reproduction response puzzle, as all of the studied species are known for strong vegetative reproduction (Filippova and Thormann, 2015; Leiřová-Svobodová et al., 2018; Stenström, 1999).

The formation of generative organs like flowers and fruits with seeds is a nutrient-demanding process, which must be preceded by long enough period of above and belowground vegetative organs growth and development (Sletvold and Ågren, 2015). Sedges occurring in peatlands like *Eriophorum vaginatum* are perennial plants, which overwinter in the form of rhizomes and start to form roots and leaves once the conditions are favorable (Wein, 1973). Leaves of *Eriophorum vaginatum* start to grow earlier, and the maximal leaf biomass is developed sooner when the ambient temperature is higher. The root growth also begins earlier in warmer conditions (Sullivan and Welker, 2005). Earlier establishment on site, root development, and shading of the ground by maximally developed leaf mass may give the plant a competitive advantage in such nutrient-poor environments like peatland (Damgaard and Weiner, 2017).

The growing season of plants in high latitudes is usually prolonged by warming more than those in mid and low latitudes (Ruosteenoja et al., 2016). However, a multifactorial study conducted in two peatlands in different latitudes found that only forbs in mid-latitude fen took advantage of warmer air and the growing period of sedges or shrubs in mid-latitudes and none of the plant functional groups in the fen above the arctic circle were influenced by higher temperature (Mäkiranta et al., 2018). The mean daily temperature is not the only factor influencing the length of the growing season. The length of the day is a very important factor sensed by buds, which is not changing with climate change. Therefore, annual plants are more likely to take advantage of earlier onset of higher temperature if their seeds are not photoblastic (Galvão and Fankhauser, 2015). The variations among the responses of plants in different latitudes may be ascribed to the different degrees of seed dormancy, which may not always be broken by the right temperature (Penfield, 2017). Plants in the harsher environment of the arctic region had to evolve better protection from germinating in suboptimal conditions, which would mean loss of progeny (Jurado and Flores, 2005).

Changes in precipitation patterns and higher evapotranspiration are expected results of climate change, which may cause a lowering of the water table in peatlands. The growing period of sedges was prolonged regardless of latitude in the study of Mäkiranta et al. (2018) when water table level was deeper, but shrubs and forbs were not affected by the drop in water table. Leaf biomass development of peatland plants is typically fast, and it

declines more gradually until the end of vegetation season. Therefore, earlier reaching of maximum leaf area implies a longer period of photosynthetic activity and accumulation of carbohydrates (Wilson et al., 2007). Timing of maximum leaf area occurrence was not observed to change by higher temperature, but the maximal leaf area developed sooner in the mid-latitude fen, while later in an arctic fen in response to warmer ambient air (Mäkiranta et al., 2018).

The studies of peatland vegetation phenological responses are performed for a rather short period of time. Such studies may not provide the full insight into changes coming with climate change, as short-term and long-term phenological responses of plants in the boreal region may differ. Although drawing general conclusions based on one site experiment is almost impossible, as plants of different latitudes may utilize diverse strategies in reaction to altered environmental conditions (Arft et al., 1999), conducted studies provide a clue about the direction of changes, which can be expected in the warmer future world. However, when making predictions about the plants' developments in the future, it is necessary to remember that the magnitude of actual changes in phenological events may be greater than the changes observed in the climate change experiments (Wolkovich et al., 2012).

2.1. Use of remote sensing in peatland vegetation phenology detection

Studying plant phenology by classical, personal observation-based approach in the remote areas with almost impenetrable terrain of peatlands is a very complicated task. Digital repeat photography overcomes the need for the daily personal presence of the researcher on-site and provides information about the greening, peak of the green biomass occurrence, and senescence of vegetation. If the camera's field of view is synchronized with the eddy covariance flux tower, information about the biomass can be linked with vegetation photosynthetic activity (Koebisch et al., 2020; Peichl et al., 2015). However, due to involvement of several environmental factors, the obtained data with controlled climate change scenarios is insufficient to provide clear idea of phenological changes under changing climate. Therefore, information about the timing of main phenological events in different temperatures must be obtained by comparing different years. This approach was used to reveal that the growing period of mosses and vascular plants in mid-latitude peatland starts sooner when the spring temperature is higher (Peichl et al., 2015).

Some areas of peatland occurrence are so remote that the only way of monitoring is remote sensing through satellites. Vegetation indices such as Normalized Difference Vegetation Index (NDVI) are a useful tool to obtain information about the beginning or the peak of a vegetation season. They may be used not only for satellite remote sensing but also for ground measurements in climate change experiments (May et al., 2020). Despite the wide availability of satellite products for NDVI calculation with fair spatial and temporal resolution (Cao et al., 2018), one must be careful when monitoring peatland vegetation. Changes in NDVI are well-correlated with the phenology of vascular plants but poorly correlated with mosses (Buttler et al., 2015). Therefore, vegetation composition must be taken into account while interpreting signals to prevent the overestimation of carbon fixation by peatlands (Yuan et al., 2014). Areas covered by *Sphagnum* spp. and vascular plants can be distinguished using satellite remote sensing products of green, near-infra-red, and short-wave infra-red regions (Schaeppman-strub et al., 2008).

The boreal region, where most northern peatlands occur, is covered by snow for a considerably long period of the year. Monitoring of plant phenology, especially phenology of evergreen species, by NDVI might be less reliable due to differences in values at the beginning of vegetation season caused rather by snow-melt than by green-up of plants. Plant phenology index (PPI) was developed and tested for tracking the phenology of boreal region vegetation and was observed to perform better than NDVI (Jin and Eklundh, 2014; Karkauskaite et al., 2017). Therefore, PPI may be a good option for remote sensing of peatland vegetation phenology.

Backscattering of different waves is a general phenomenon used by meteorologist and environmental scientist to predict the status of Earth

vegetation. Different measurements including the satellite remote sensing techniques are used to compare the vegetation status between years and prediction of future change based on past variations in climate and the reactions of plants to them (Jones et al., 2011). Passive microwave remote sensing can be more precisely applied to predict the phenological cycles of short vegetation like the one in peatlands (Jones et al., 2011). Peatland is also inhabited by evergreen shrubs and mosses, which at the beginning and end of vegetation season may be difficult to assess by reflectance-based vegetation indices only. Sun-induced chlorophyll fluorescence (SIF) is a remote sensing technique utilizing the properties of the photosynthetic apparatus of plants. SIF was proven to be useful for peatland plant communities distinguishing, but thanks to its direct link to photosynthesis and possibility to use from ground through drone and airplane to satellite level, it has high potential to be used for phenological studies in peatlands (Bandopadhyay et al., 2019, 2020).

3. Changes in peatland vegetation composition

The prevailing climatic conditions are the main driver of the vegetation composition of ecosystems (Sonesson et al., 2002). Vegetation composition is a major characteristic of any ecosystem, and functions of the ecosystem are linked to it (Carrick and Forsythe, 2020). The ecosystem can support the important functions only as long as it possesses sufficient species richness and diversity of functional traits (Robroek et al., 2017b). Biodiversity is a key to the resistance and resilience of ecosystems and to fulfilling ecosystem services in altered climatic conditions (Cardinale et al., 2012; Isbell et al., 2015). Land-use and climate change are the most important drivers of changes in vegetation composition and biodiversity (Sala et al., 2000). If species fail to acclimate or adapt to altered climatic conditions, they need to either move to more favorable conditions to survive. Plants as sessile organisms relocating by reproductive organs may fail to keep pace with the speed of environmental changes. Moreover, the fragmented nature of mid-latitude peatlands and the fact that boreal peatlands span to the edge of the terrestrial surface makes it impossible for plants of these ecosystems to relocate to a more suitable place once the climate changes in their actual location. Therefore, they are left only with two options: adjust to new conditions or go extinct (Corlett, 2016; Xu et al., 2018). Losing one species generally does not pose a threat to the ecosystem, but losing a plant functional group may mean the total change of ecosystem type (Hooper et al., 2012). The species with distinct traits are more valuable to the ecosystem than species possessing the traits common to several species (Robroek et al., 2017b). Peatlands are globally the most homogenous natural ecosystems with very similar vegetation composition among various wetlands in different parts of the globe (Carrick and Forsythe, 2020). Northern peatlands consist of a relatively small number of species with complex relationships and contrasting responses to climate change (Walker et al., 2015). Because of the strong role of the vegetation itself in sustaining a favorable environment, the substantial changes in vegetation are the result of crossing the tipping points in abiotic parameters, for example the depth of water table level (Lamentowicz et al., 2019). Based on responses of species to climate change the majority of northern peatlands plants can be divided into two groups with strongly correlated responses between species within the group. However, some of the major species, such as *Eriophorum vaginatum* or *Sphagnum magellanicum*, have distinct reactions to climate change non-correlated to other species (Robroek et al., 2017b).

Species of genus *Sphagnum* are recognized as creators of conditions inevitable for peatland formation; hence this genus is essential for peatland formation initiation and to keep the environment with high carbon storage potential (van Breemen, 1995). *Sphagnum* spp. are also the main engineers of distinct hummock-lawn-hollow (patches of the elevated, flat, and lowered surface) topography of peatlands. Different *Sphagnum* spp. inhabit different elevations above the water table (Bragazza, 2006; Yang et al., 2019). The ability of *Sphagnum* spp. to fulfill the abovementioned functions in the future is endangered as the studies report decreasing abundance of different *Sphagnum* spp. with increasing temperature (Bragazza et al.,

2016; Dieleman et al., 2015; Łuców et al., 2017; Lyons et al., 2020; Norby et al., 2019; Weltzin et al., 2003) and decreasing water table (Jassey et al., 2018), which are the consequences of climate change (IPCC, 2021). The increasing temperature does not always result in a negative effect on peat mosses. The moderately higher temperature in the arctic region enhances the length growth and biomass production of widespread *S. fuscum* (Dorrepaal et al., 2004). Moreover, the trend in precipitation amount is impossible to generalize. Some regions of the world will experience a higher amount of precipitation (IPCC, 2021). When the water availability increases, the abundance of *Sphagnum* spp. is also higher (Jassey et al., 2018) because their length growth is enhanced (Sonesson et al., 2002).

Peatlands are usually inhabited by more than one *Sphagnum* spp. at each topographical position; therefore, the decreasing abundance of one species may not endanger the ecosystem balance if other species with similar traits colonize the niche (Robroek et al., 2017b). Despite *Sphagnum* spp. are generally considered as desiccation-avoiding species, the water management strategy of hummock and hollow species differs. Due to their growth in compact clusters, the hummock species are able to conduct water from the deeper water table and may take advantage of warmer weather usually connected with dry periods, which occur in the summer months. Therefore, despite their lower overall growth rates, hummock species are especially important during drier months, when the productivity of hollow species is hampered by lower water tables (Asada et al., 2003; Bengtsson et al., 2021). However, the biomass production of *Sphagnum* spp. or *Polytrichum strictum* is normally negatively correlated to the distance from the water table (Weltzin et al., 2001). Although the peatland ecosystem is surprisingly stable and developmentally older peatlands are very resilient (Backéus, 1972; Oke and Hager, 2020; Turetsky et al., 2012), the occurrence of climate extremes like heat waves may lead to irreversible damage and die-off of hummock *Sphagnum* spp., which are not well adapted to drying. This impacts the carbon uptake of peatland as death zones, which cannot be colonized due to unfavorable elevation above water table by hollow or lawn *Sphagnum* spp. appear in carpet and persist for years after heatwave occurrence (Bragazza, 2008).

The dependence of different *Sphagnum* spp. on specific climate, especially water availability, is so pronounced that changes in *Sphagnum* spp. abundance in peat can be used to reconstruct the local or global climate (Jassey et al., 2018). Whenever in history, the conditions in peatlands shifted towards wetter *Sphagnum cuspidatum* became more abundant. On the other hand, *Sphagnum papillosum* and *Sphagnum imbricatum* are associated with dry conditions (Mauquoy et al., 2002a; Van Geel et al., 1996). These findings are in accordance with the modern climate manipulation experiments, which found decreasing abundance of *Sphagnum cuspidatum* and increasing abundance of *Sphagnum papillosum* in drier conditions (Breeuwer et al., 2009; Robroek et al., 2007a).

Not only changes in abiotic conditions present a challenge for *Sphagnum* spp., changes in biotic conditions, especially competition by vascular plants, are at least an equal threat. Although, the relationship between peat mosses and vascular plants is very complex. *Sphagnum* development from diaspores and subsequent growth is increased by vascular plants cover, which provides a more stable microclimate in water deficit conditions (Buttler et al., 1998). Sparse cover of vascular plants decreases the wind speed directly above the *Sphagnum* surface, hence decreasing the evapotranspiration and improving the water use efficiency by mosses (Heijmans et al., 2001). However, denser vascular plant canopy deprives underlying *Sphagnum* spp. of necessary light and causes their death (Bragazza et al., 2015; Chong et al., 2012). *Sphagnum* spp. can, to some extent, control the growth of vascular plants by limiting the nutrient availability, as the atmospheric deposition goes firstly through the moss layer and only then reaches the roots of vascular plants. Nevertheless, increasing temperature enhances mineralization and nutrient availability in the zone of vascular plants roots, out of reach of *Sphagnum* spp. (Dorrepaal et al., 2006; Malmer et al., 1994; van Breemen, 1995). Hence, a higher mineralization rate gives a competitive advantage to vascular plants and makes it difficult for mosses to control the environmental conditions (Malmer

et al., 1994, 2003). The growth of shrubs' fine roots is also increased in warmer and drier conditions, enabling shrubs to acquire more available nutrients (Malhotra et al., 2020). In addition, a warmer climate enhances the growth of mycorrhizal fungi, which makes more nutrients available to ericaceous shrubs, giving them another advantage over mosses (Asemaninejad et al., 2018; Bragazza et al., 2013). The increasing temperature has also a direct effect on the *Sphagnum*-vascular plants' relationship. While low, creeping shrubs may be overgrown in warmer conditions by *Sphagnum*, the growth of higher shrubs will be enhanced enough to compete with peat mosses (Dorrepaal et al., 2006).

The vascular plants are not the sole competitors of mosses. One species of *Sphagnum* may suppress the other *Sphagnum* spp. as well. Although the increase in temperature improves the growth of various species, hummock species can outcompete the hollow ones and become more abundant in moss carpets. The *Sphagnum* spp. occurring in the mid-latitude peatlands will in warmer world replace the species occurring in more northern peatlands (Breeuwer et al., 2008; Gunnarsson et al., 2004; Robroek et al., 2009). The studies of Gunnarsson et al. (2004) and Breeuwer et al. (2008) are a good example of the importance of biotic components when evaluating abiotic factors as *S. balticum* competitive strength was found to be enough for outcompeting *S. fuscum* and *S. magellanicum*, but the species was suppressed by *S. papillosum*, in higher temperature conditions. The changes in vegetation composition do not depend on the reaction of one species. Despite *S. magellanicum* was found to grow faster in warmer and slower in drier conditions (Robroek et al., 2007b), outperforming other species in drier and being outperformed in warmer conditions was reported (Breeuwer et al., 2008; Robroek et al., 2007a). *Sphagnum* spp. react to fluctuating water table levels in the same manner as to its constant drop (Breeuwer et al., 2009). Nevertheless, the species growing in higher topographic positions, e.g., lawn and hummock species, generally possess stronger competitive capacity even in high water table level conditions. The competition is stronger when the water table drops, which causes the increased abundance of lawn species in hollows and typical hummock species in low hummocks (Robroek et al., 2007a). Although the competition among species is considerable, the survival of individual plants of the peatland mosses depends on being surrounded by other mosses. Some *Sphagnum* spp. may grow faster when they are surrounded by other than their own moss species, like in the case of *S. fuscum* growing among *Dicranum elongatum* (Sonesson et al., 2002).

Different vegetation composition of bogs and fens causes different reactions to climate change, but the hampered growth of mosses and improved growth of vascular plants in dryer conditions is a common feature. Warming causes higher biomass increment of shrubs and slower growth of sedges in bogs, but in fens, sedges grow better when the temperature is higher (Weltzin et al., 2000). Sedges of genus *Carex* are together with *Eriophorum vaginatum*, the most widespread graminoids in northern peatlands (Bedford et al., 1988; Bernard and Hankinson, 1979; Robroek et al., 2017b). With increasing temperature, *Carex* spp. are becoming more abundant in fens at the expense of *Sphagnum* spp. (Dieleman et al., 2015; Łuców et al., 2017). Other sedges, like *Eriophorum vaginatum* and *Scheuchzeria palustris*, also thrive in warmer fens and increase their range (Weltzin et al., 2003). Sedges in fens are able to take advantage of different changes in water availability. While *Trichophorum cespitosum* thrives in dryer conditions, *Carex lasiocarpa* and *Carex livida* take advantage of a wetter environment (Mäkiranta et al., 2018; Weltzin et al., 2003). Moreover, *Eriophorum vaginatum* does spread to niches previously occupied by shrubs when the water table level increases (Jassey et al., 2018). However, sedges inhabiting bogs cede the space to shrubs when a longer period of drought causes water table level fluctuation (Breeuwer et al., 2009). The reactions of *Carex lasiocarpa* to drought depend on the severity or length of the drought period. If plants of this sedge are subjected to longer drought, their growth is hampered, and vegetative reproduction is reduced. Plants start to focus more on the production of aboveground biomass, leaves get thicker, and physiological changes occur (Yuan et al., 2017). When the precipitation-evapotranspiration relationship changes in prospect to evapotranspiration, causing the drop of the water table for more than a decade, all

peatland plants struggle and start to diminish, while the bare litter patches become more abundant (McPartland et al., 2019b).

Forbs are the plant functional group, which is the most prone to diminish from peatlands under changed climatic conditions. Studies report that increasing temperature (McPartland et al., 2019a) and rising as well as falling water table (McPartland et al., 2019b) cause a lower abundance of different forbs. One of the reasons for their disappearance from warmer peatlands is probably the damage on photosynthetic apparatus and subsequent substantially lower photosynthetic activity of forbs than other plant functional groups (Rastogi et al., 2019).

The most morphologically, physiologically, and systematically variable group of peatland vegetation are shrubs. Thanks to their relatively high variability, some species can take advantage of increasing temperature while others are impacted negatively. Species of the *Andromeda* genus may become more abundant in the future warmer world, but *Kalma polifolia* will become rarer (Buttler et al., 2015; Weltzin et al., 2003). The temperature-related changes in abundance of *Vaccinium* spp. depend on the developmental stage of peatland and the current climatic conditions. Warming of mid-latitude bog without tree cover or near-arctic fen results in a higher abundance of *Vaccinium* spp. (Bragazza et al., 2016; Wiedermann et al., 2007). However, decreasing abundance with increasing temperature was found in mid-latitude bog dominated by trees and in mid-latitude fen (Buttler et al., 2015; McPartland et al., 2020). Peatlands inhabiting shrubs, in general, expand in drier conditions (Table 2), which is proven by the negative effect of higher water table level on the abundance of *Vaccinium oxycoccus* (Jassey et al., 2018). The ongoing climate change favors most of the shrubs of peatlands, and they are becoming more abundant (Gunnarsson et al., 2002). Additionally, the denser cover of shrubs, together with warmer and drier conditions, provide suitable conditions for tree seedling establishment. Subsequently, tree cover further increases the density of the shrub canopy. Such positive feedback slowly changes *Sphagnum*-dominated peatland to the forest (Holmgren et al., 2015). Afforestation of peatlands will be triggered rather by increasing temperature than by decreasing precipitation or longer and more often occurring drought events (Heijmans et al., 2013).

The climate change manipulation experiments provide useful information about the most probable changes in peatland vegetation in a future changed climate. However, the experiments are done just over small patches of peatland and observe only the vegetation already existing in the peatland. Global climate change will create in peatland suitable conditions for species that are not yet present. These new plants will probably be the most significant factor shaping future peatlands and the reactions of plants to climate change (Alexander et al., 2015; Bragazza et al., 2016). When the change in vegetation occurs, it will not be a slow process taking centuries but rather a rapid shift of vegetation types or ecosystems (Loisel and Yu, 2013; Pellerin and Lavoie, 2003).

3.1. Common techniques used for peatland climate manipulation

Over the years, several different techniques have been used to simulate the possible future climatic conditions in peatlands. The increase in temperature was reached by either passive methods, like open-top chambers or warming chambers, or by active methods such as infrared heaters, heating in glasshouses, or propane-fueled heaters (Table 2). Passive warming is a cost-effective way of increasing the air temperature. However, warming is higher during the day than at night, and unwanted cooling of the peat may occur due to increased evapotranspiration caused by warming up the air (Dabros et al., 2010; Górecki et al., 2021). Therefore, passive warming simulates future climate change only partially. Active methods, especially a combination of active and passive heating, allow for more precise and stable manipulation but come with higher running costs and more laborious maintenance (Aronson and McNulty, 2009). A unique method was used by Bragazza et al. (2016) when whole blocks of vegetation with the peat below were transplanted from higher latitude to lower latitude bog, changing the temperature and precipitation regimes. However, the vegetation

Table 2
Changes in abundance of peatland plant species caused by simulated climate change.

Climate factor (change)	Time period	The method used for manipulation	Type of peatland	Changes in species abundance		References
				Increased abundance	Decreased abundance	
Temperature (increase)	1 year	Increased temperature in the greenhouse	Fen	<i>Carex disperma</i> ♦ <i>Carex magellanica</i> ♦	<i>Sphagnum</i> spp. ●	(Dieleman et al., 2015)
Temperature (increase)	4 years	Open-top chambers	Bog	<i>Andromeda polifolia</i> ■	<i>Vaccinium oxycoccos</i> ■	(Buttler et al., 2015)
Temperature (increase)	9 years	Warming chambers	Fen	<i>Vaccinium oxycoccos</i> ■ <i>Eriophorum vaginatum</i> ♦		(Wiedermann et al., 2007)
Temperature (increase)	3 years	Warming chambers	Fen	<i>Sphagnum papillosum</i> ●	<i>Sphagnum balticum</i> ●	(Gunnarsson et al., 2004)
Temperature (increase)	4 years	Infrared heat lamps	Bog	<i>Andromeda glaucophylla</i> ■	<i>Sphagnum</i> sect. <i>Acutifolia</i> ● <i>Kalmia polifolia</i> ■	(Weltzin et al., 2003)
Temperature (increase)	1 year	Open-top chambers	Fen	<i>Scheuchzeria palustris</i> ♦	<i>Sphagnum angustifolium</i> ●	(Lyons et al., 2020)
Temperature (increase)	154 days	Increased temperature in the greenhouse	Unspecified	<i>Sphagnum balticum</i> ●	<i>Sphagnum fuscum</i> ● <i>Sphagnum magellanicum</i> ●	(Breeuwer et al., 2008)
Temperature (increase)	2 years	Propane-fired heat exchangers for air and low-wattage heaters for peat	Bog	Shrubs ■	Forbs □	(McPartland et al., 2019a)
Temperature (increase)	3 years	Propane-fired heat exchangers for air and low-wattage heaters for peat	Bog		<i>Sphagnum angustifolium</i> ● <i>Sphagnum fallax</i> ● <i>Sphagnum magellanicum</i> ●	(Norby et al., 2019)
Temperature (increase)	4 years	Propane-fired heat exchangers for air and low-wattage heaters for peat	Bog		<i>Vaccinium oxycoccos</i> ■ <i>Menyanthes trifoliata</i> □	(McPartland et al., 2020)
Temperature (increase)	1 year	Infrared heaters	Fen	<i>Carex limosa</i> ♦ <i>Carex rostrata</i> ♦	<i>Sphagnum angustifolium</i> ● <i>Sphagnum teres</i> ●	(Łuców et al., 2017)
Temperature (increase) and precipitation (decrease)	3 years	Transplanting of mesocosms from higher to lower altitude	Bog	<i>Vaccinium uliginosum</i> ■	<i>Sphagnum fallax</i> ● <i>Eriophorum vaginatum</i> ♦	(Bragazza et al., 2016)
Water table level (decrease)	1 year	Regulated in mesocosm	Fen	<i>Kalmia polifolia</i> ■ <i>Ledum groenlandicum</i> ■		(Dieleman et al., 2015)
Water table level (decrease)	4 years	Regulated in mesocosm	Bog	<i>Andromeda glaucophylla</i> ■ <i>Chamaedaphne calyculata</i> ■		(Weltzin et al., 2003)
Water table level (decrease)	3 years	A ditch dug around the plot	Fen	<i>Betula nana</i> ■ <i>Vaccinium oxycoccos</i> ■ <i>Trichophorum cespitosum</i> ♦ <i>Sphagnum subnitens</i> ●	<i>Menyanthes trifoliata</i> □ <i>Equisetum fluviatile</i> □	(Mäkiranta et al., 2018)
Water table level (decrease)	12 years	A ditch dug around the plot	Fen	No vegetation points	Mosses ● Graminoids ♦ Shrubs ■ Forbs □	(McPartland et al., 2019b)
Water table level (decrease)	27 months	Addition of 10 cm of peat under vegetation	Fen	Vascular plants ■♦	<i>Sphagnum</i> spp. ●	(Jassey et al., 2018)
Water table level (decrease)	16 months	Regulated in mesocosm	Bog	<i>Sphagnum papillosum</i> ● <i>Sphagnum magellanicum</i> ● <i>Sphagnum austinii</i> ●	<i>Sphagnum cuspidatum</i> ● <i>Sphagnum cuspidatum</i> ● <i>Sphagnum rubellum</i> ●	(Robroek et al., 2007a)
Water table level (fluctuation)	2 years	Regulated in mesocosm	Bog	<i>Sphagnum magellanicum</i> ● Shrubs ■	<i>Sphagnum cuspidatum</i> ●	(Breeuwer et al., 2009)
Water table level (increased)	12 years	Water pumped into the plot	Fen		Graminoids ♦ Mosses ● Shrubs ■ Forbs □	(McPartland et al., 2019b)
Water table level (increased)	27 months	Removal of 10 cm of peat below vegetation	Fen	<i>Sphagnum</i> spp. ● <i>Eriophorum vaginatum</i> ♦	<i>Vaccinium oxycoccos</i> ■	(Jassey et al., 2018)
Water table level (increase)	4 years	Regulated in mesocosm	Fen	<i>Carex lasiocarpa</i> ♦ <i>Carex livida</i> ♦		(Weltzin et al., 2003)

Graminoid ♦ shrub ■ forb □ moss ●.

Note: Only significant increase or decrease in species or plant functional group caused by climate factors are shown in the table.

was suddenly exposed to different climatic conditions and new vegetation community, which is not the precise simulation of climate change.

Water table depth was manipulated either in the controlled conditions with relatively precisely defined depth or in natural conditions, by digging ditches or removing the underlying layer of peat to decrease the water table level or adding peat under vegetation or pumping water into the plot of vegetation to increase the level of the water table (Table 2). The manipulation in mesocosms permit for more precisely defined and stable water table level, but is possible only with small patches of vegetation, and the water is mostly added in the form of artificial solution (Breeuwer et al., 2008, 2009; Dieleman et al., 2015; Robroek et al., 2007a). The addition of water from ditch dug in the original peatland is more laborious but expose the vegetation to more natural conditions (Weltzin et al., 2003). Water table level manipulations in situ allow for altering the water regime for larger patches of vegetation and ensure the natural supply of the water. Nonetheless, the water table level by in situ manipulation is less controlled

by scientists and more dependent on the natural conditions of the site (Mäkiranta et al., 2018; McPartland et al., 2019b).

Different climate and water table depth manipulation methods have their advantages and disadvantages. The exact simulation of the future is impossible due to its uncertain scale and the complicated relationships of ecosystem components with climate. However, the combination of temperature and water regime manipulation provides a more truthful perspective than the change of only one climate variable and in situ manipulation better considers the complexity of nature. A combination of active and passive methods, like in McPartland et al. (2019a), may be necessary to achieve realistic manipulation of the climate.

4. Impact of changes in peatland vegetation on carbon balance

Northern peatlands belong to ecosystems with the highest potential to enhance the pace of climate change by positive feedback due to their

large carbon stock and location in the most rapidly warming region of the globe (Gorham, 1991; Hoegh-Guldberg et al., 2018). Whether the ecosystem is a sink or source of carbon in relation to the atmosphere depends on rates of carbon uptake and release. Carbon is taken up through photosynthesis and released by respiration and methane release. Ecosystem photosynthesis, known as gross primary production, is influenced by the vegetation composition, physiological status of its components, and the length of photosynthetic activity (Laine et al., 2012; Lund et al., 2010). Ecosystem respiration also depends on vegetation composition and the physiological status of plants. Additionally, the respiration of peatlands depends on hydrology, composition, amount, and activity of microorganisms, and the quality of litter (Juszczak et al., 2013; Acosta et al., 2017; Górecki et al., 2021; Laiho, 2006). Methane release is determined by rates of methanogenesis and methanotrophy, which both depend on microbial activity, litter quality, water table depth, temperature and vegetation composition (Riutta et al., 2007; Whalen, 2005; Juszczak and Augustin, 2013). All of the abovementioned factors will change with climate change, and all of them will shape the future climate. Climate change-induced changes in vegetation and their impact on the carbon balance of peatland must be included in climatic models; otherwise, models underestimate the scale and pace of changes (Cox et al., 2000; Müller and Joos, 2021).

4.1. Carbon fixation

Length of vegetation season belongs to the most important parameters influencing gross primary production of peatlands (Lund et al., 2010). Temperature is a major factor influencing carbon assimilation in northern peatlands. Enhanced carbon fixation with increasing temperature is predicted in mid- and high latitude peatlands as a result of longer vegetation season (Gallego-Sala et al., 2018; Peñuelas et al., 2004). However, the increasing temperature cannot prolong the vegetation season of high latitudes infinitely. Photosynthetically active radiation is a critical factor for carbon assimilation. The availability of light in high latitudes is not constrained only by shading or clouds but also by the length of days during the winter half of the year, which are not predicted to change (Gallego-Sala et al., 2018). Cloud shading and aerosol thickness are also significant factors decreasing the carbon uptake by peatlands, but it is difficult to predict what changes in cloud cover and aerosol presence climate change will bring (Harenda et al., 2021; Nijp et al., 2015). Although phenology is closely linked to climatic conditions, it is better correlated with the rate of carbon uptake than any of the climatic variables itself (Järveoja et al., 2018). The effect of climate warming on peatland gross primary production is mediated through vegetation phenology, especially sooner green-up during spring and later senescence in autumn (Koebsch et al., 2020). Plant phenology is influenced by the compound effect of abiotic factors; therefore, it is the most significant factor controlling the maximal rate of gross primary production of peatland (Peichl et al., 2018).

The beginning of vascular plants' vegetation season is an important event impacting carbon uptake and net ecosystem exchange of carbon (Peichl et al., 2015). Increased temperature triggers sooner spring growth of graminoids and earlier full leaf biomass establishment, which prolongs the period of photosynthetic activity (Sullivan and Welker, 2005). The decreased water table level also prolongs the vegetation period of graminoids, probably by enhancing warm-up of the top layer of peat and by improved aeration (Mäkiranta et al., 2018). Graminoids play a crucial role in fens' gross primary production (Robroek et al., 2017a). Increasing temperature favors the growth and expansion of graminoids of fens as long as the water table is high enough (Table 2). Therefore, fens can, in the future, potentially fix more carbon during the vegetation season in the areas where precipitation will not become lower than evapotranspiration (Li et al., 2021; Robroek et al., 2017a). However, *Sphagnum*-dominated fens are a significantly stronger sink of carbon than graminoids-dominated fens due to a longer period of photosynthetic activity and a higher ratio of assimilation to respiration (Glenn et al., 2006). Peat mosses start the photosynthetic activity as the first plants of peatland vegetation because of their "evergreen" nature and low temperature requirements for physiological activity.

Evergreen shrubs begin vegetation season shortly after mosses when the top layer of peat warms up. The vegetation season of graminoids and forbs starts later after they produce leaves. The contribution of plant functional groups to peatland carbon assimilation follows the pattern of the beginning of their photosynthetic activity (Korrensalo et al., 2016; Moore et al., 2006). The changes caused by climate change will likely have opposite effects on carbon assimilation by peatland vegetation in spring. Decreasing cover of *Sphagnum* spp. will decrease the carbon uptake, but the sooner start of the physiological activity of vascular plants may erase this decrease and possibly increase the carbon assimilation during the spring green-up (Tables 1, 2).

Mosses of genus *Sphagnum* are an important contributor to overall gross primary production. Despite their relatively low level of photosynthetic apparatus light saturation, they are responsible for a substantial part of maximal gross primary production (Peichl et al., 2018). *Sphagnum* spp. are also the most important component of the peatland vegetation for resistance and resilience of carbon accumulation to drought (Kuiper et al., 2014). However, some species of *Sphagnum* cope with climate change better than others. While carbon assimilation of hummock species *S. medium* continues at the same rate under warmer and drier conditions, carbon assimilation of hollow species *S. fallax* drops rapidly (Jassey and Signarbieux, 2019). Growth of *S. fallax* is then hampered, and species can be overgrown by better performing *Sphagnum* spp. (Rastogi et al., 2020). Increasing cover of vascular plants reported by climate manipulation studies (Dieleman et al., 2015; Jassey et al., 2018; Weltzin et al., 2003; Wiedermann et al., 2007) reduces the productivity of *Sphagnum* spp. (Bragazza et al., 2013). The production reduction by vascular plants cover is even higher than the reduction caused by water level drop (Bengtsson et al., 2021). Shrubs are the plant functional group of peatland vegetation, which is the most responsible for the reduction of photosynthesis. Hence, the increasing cover of shrubs in bogs due to climate changes will decrease the rate of assimilated carbon. However, the presence of shrubs decreases not only the carbon assimilation but the overall carbon turnover, and the net ecosystem exchange is not significantly impacted (Ward et al., 2009). In addition to mosses photosynthesis reduction, shrubs cause the lowering of peatland carbon exchange by their slow photosynthesis and respiration relative to mosses or graminoids. Higher carbon assimilation and accumulation by shrubs can be expected in the future, as shrubs' gross primary production is higher when precipitation events are less frequent. Longer periods between rains lower the photosynthesis of mosses and graminoids (Adkinson and Humphreys, 2011; Radu and Duval, 2018). In general, the photosynthetic activity of vascular plants increases with warmer and drier conditions, but the photosynthetic activity of *Sphagnum* spp. dramatically decreases (Bragazza et al., 2016). The beginning, end, and length of the growing season are significant factors for the amount of assimilated carbon per year, but the leaf area index of vascular plants is even stronger correlated with gross primary production than abiotic or phenological variables. Therefore, changes in vegetation composition towards more vascular plants abundance will probably lead to higher assimilation of carbon from the atmosphere to plant biomass (Gavazov et al., 2018; Lund et al., 2010; Ward et al., 2013).

Some of the northern peatlands lay in the locations where the soil is permanently frozen for years with the minimal physiological activity of plants. Permafrost peatlands, which contain a large amount of carbon, are thawing, which makes the stored carbon available for decomposers, but also creates the conditions for colonization by plants. The carbon accumulation of newly thawed peatlands rapidly increases, and carbon dioxide uptake exceeds its release, but such peatlands are a substantial source of methane, which may make them a net contributor to global warming for decades (Swindles et al., 2015; Turetsky et al., 2007).

In addition to plant photosynthesis, microbial photosynthesis is an important contributor to peatland carbon fixation. Although the presence of specific phototrophic microorganisms depends on vegetation composition, the carbon fixation rate by microbes remains similar for different communities and climatic conditions. However, microbial photosynthesis is related to the presence of *Sphagnum* spp. and will probably decline with the

diminishing of peat mosses and increasing temperature (Basińska et al., 2020; Hamard et al., 2021).

4.2. Respiration

Peatland microbiota is strongly connected to the plants occurring in the peatland. Occurrence and ratios between fungi and bacteria or different groups of bacteria depend on the litter properties, which ultimately depend on the vegetation composition (Bragazza et al., 2015). The impact of changes in abiotic conditions on litter quality is mainly mediated via changes in vegetation composition (Straková et al., 2010). The litter of *Sphagnum* spp. is decomposed significantly slower than the litter of other plant functional groups of peatland vegetation (Dorrepaal et al., 2005). Slower *Sphagnum* spp. litter decomposition is caused by the lower enzymatic activity of microorganisms in it, especially carbon-acquiring enzymes (Strakova et al., 2011). On the contrary, the residuals of forbs are decomposed the fastest of all plant functional groups of peatlands. The decomposition rate of vascular plants litter is increasing in a warmer climate (Dorrepaal et al., 2005). Higher carbon release from vascular plants litter compared to *Sphagnum* spp. litter is caused by both higher aerobic and anaerobic decomposition, which increase with higher temperature (Duval and Radu, 2018). However, not all *Sphagnum* spp. decompose at the same speed. Hummock species with their higher cellulose: hemicellulose and structural: metabolic carbohydrates decompose slower than hollow species (Straková et al., 2010).

Phenolic compounds belong to one of the most important groups of compounds related to peat properties. The role of phenolic compounds in peatland carbon balance is very complex. *Sphagnum* spp. polyphenols are part of cell walls and persist as a part of litter instead of leaching to the pore water. Contrastingly, vascular plants produce easily leachable polyphenols or exude polyphenolic compounds by roots, which persist in pore water (Dieleman et al., 2016; Dorrepaal et al., 2005). While relatively simple phenolic compounds produced by the roots of vascular plants lower the microbial carbon use efficiency resulting in higher carbon dioxide release, polyphenols present in *Sphagnum* spp. or shrub leaves decrease the population of microbes and carbon release by reducing nitrogen availability (Bragazza et al., 2013; Dieleman et al., 2015; Frey et al., 2013). Low pH created by *Sphagnum* spp. protects phenolic compounds from degradation by lowering phenol oxidase activity in wet as well as dry conditions. Graminoid peat provides conditions for higher phenol oxidase activity, which increases in drier conditions. With less peat moss litter and more graminoid peat, phenolic compounds will degrade faster, and peat will be more prone to decomposition (Williams and Yavitt, 2000).

Emission of carbon dioxide from *Carex* spp. dominated peatlands is significantly higher than from *Sphagnum*-dominated peatlands because *Carex* spp. provide litter of higher quality with narrower carbon: nitrogen ratio (Lyons and Lindo, 2020). Higher ecosystem respiration of graminoid-dominated peatlands is also driven by the higher amount of dissolved organic carbon compared to *Sphagnum* spp. dominated peatlands. Dissolved organic carbon stimulates the activity of microbiota and the decay of litter. Increasing the abundance of graminoids at the expense of peat mosses will very likely stimulate the decomposition and enhance the carbon release from fens (Dieleman et al., 2015). When vascular plants become more abundant and peat mosses less abundant in a future warmer climate, ecosystem respiration may increase because the litter of vascular plants decomposes faster than *Sphagnum* spp. litter due to higher carbon lability (Bell et al., 2018; Bragazza et al., 2016; Del Giudice and Lindo, 2017; Mao et al., 2018). Warming enhances decomposition and respiration also through the reduction of predators like testate amoebae, which in turn cause an increase in the number of bacterial decomposers (Jassey et al., 2013; Basińska et al., 2020).

A plant removal experiment suggests that graminoids are mostly responsible for respiration increase, and dwarf shrubs like *Caluna vulgaris* may decrease ecosystem respiration of bogs (Ward et al., 2009). Although litter of some graminoids like *Eriophorum vaginatum* has high nitrogen and phosphorus content, which makes it ideal for fast decomposition, plants have high nutrient recycling capacity causing fast depletion of

macronutrients from peat and hampering microbial activity. Shrubs of *Vaccinium* spp. provide lower quality litter than graminoids, but because of their lower resorption of nutrients, shrub litter increase the macronutrient content of peat and enhance the microbial activity (Kaštovská et al., 2018). Litter of different species does not exist separately in the peatlands but is present in mixtures. Litter of some species like deciduous shrubs *Betula* spp. enhance the decomposition of other plants' residuals. On the contrary, *Sphagnum* spp. litter slows down the decomposition of shrubs and graminoids litter (Zhang et al., 2019). With increasing temperature and abundance of shrubs, fungi and gram-negative bacteria become more abundant. Fungi enriched communities possess more carbon degrading enzymes, which speed up peat degradation (Bragazza et al., 2015). Long-term observation from boreal peatland confirms that climate-induced vegetation changes cause decreasing carbon accumulation (Malmer et al., 2005).

4.3. Methane release

Vegetation composition is an important determinant of methane flux from peatland. The largest effect on methane release from all plant functional groups has graminoids. Graminoids influence methane flux in two ways. They produce a high amount of dissolved organic carbon molecules, which are an easy source of energy for microorganisms and their roots contain aerenchymal tissue, which conduces methane produced in catholium directly to the atmosphere without passing through acrothelm, where methane could be oxidized to carbon dioxide (Chanton, 2005; Goud et al., 2017; Moore et al., 2011; Rooney-Varga et al., 2007). The increasing abundance of graminoids in warmer fens will likely increase the methane released by their aerenchymal tissues (Dieleman et al., 2017; Noyce et al., 2014; Ward et al., 2013). Forbs with high belowground biomass may also play an important role in increasing methane emissions (Moore et al., 2011). The vegetation type also influences methane production by the litter quality. High lignin to cellulose ratio decreases the relative amount of produced methane and increases the production of carbon dioxide by microbiota (Duval and Radu, 2018). Therefore, shrub encroaching of bogs in warmer and drier future may change the ratio of produced greenhouse gasses in the prospect of carbon dioxide (Dieleman et al., 2015; McPartland et al., 2019a; Weltzin et al., 2003). The effect of abiotic factors on methane production is also modulated by vegetation. Decreased precipitation frequency together with increased rainfall per event cause higher methane release from *Sphagnum* spp. or graminoid-dominated parts of fen, but methane release of the shrub-dominated part is unaffected (Radu and Duval, 2018). Increased vascular plant cover as a result of, and together with higher temperature, cause an increase in the methane flux from the peatland (Zhang et al., 2022). The presence of graminoids increases methanogenesis, and the presence of vascular plants decreases methanotrophy. Considering the projected increasing abundance of vascular plants, methane release from peatlands will increase due to higher production and lower oxidation (Robroek et al., 2015; Table 2).

The methanogenic archaea community is closely related to peatland vegetation. Communities living in peatland dominated by *Sphagnum* spp. accumulate acetate, but graminoid-dominated peatlands are inhabited by acetoclastic methanogens (Rooney-Varga et al., 2007). In optimal conditions, *Sphagnum* spp. provide methane-oxidizing conditions and are related to lower methane release (Goud et al., 2017). However, the relationship between graminoids and methane release from peatlands is not simple and straightforward. Results from Alaskan rich fen suggest that sedges, thanks to their aerenchyma, create oxidizing conditions and support methanotrophy, which in turn lower the amount of methane present in the porewater and probably also methane release (Rupp et al., 2019). The oxidation of graminoids rhizosphere and methane release are species or genus dependent. *Carex rostrata* dominated vegetation provides less oxidizing conditions and subsequently supports higher methane release than *Eriophorum vaginatum* dominated vegetation. Even lower methane release was found from vegetation dominated by *Juncus effusus* (Strom et al., 2005).

The phenology of graminoids also influences methane release from peatlands. The earlier beginning of graminoids vegetation season, together

with its prolonging in warmer conditions, will increase the methane release (Moore et al., 2011; Sullivan and Welker, 2005).

5. Conclusions and future perspectives

Our climate is subjected to rapid changes, and ecosystems all over the world need to adapt to these changes. However, it is not only climate that is changing the ecosystems, but the changes in ecosystems also modulate the climate through positive and negative feedbacks. From a climate change point of view, the northern peatlands are one of the most important ecosystems due to their large carbon stock. Many experiments in peatlands in different countries were performed to assess the impact of future climate change on peatland vegetation and the fate of stored carbon. Those experiments were reviewed in this article and summarized in Fig. 1. Results of studies suggest that the rising temperature and altered water availability will change the vegetation phenology and composition.

As discussed in Section 2 (Changes in peatland vegetation phenology), climate warming will result in the earlier onset of shrubs and graminoids flowering. Shrubs will also increase the number of flowers, which may result in more seeds and improve their possibility for spreading. The roots of graminoids will start to grow sooner in the spring, and the leaves will develop sooner in future warmer peatlands. Drop of water table level caused by higher evapotranspiration and changed precipitation regime will prolong the vegetation season of graminoids. The short-term reaction of forbs will depend on present climatic conditions. While their vegetation season will start sooner and last longer in warmer mid-latitude peatlands, the

vegetation season will start later in the colder arctic, and its length will most probably not change.

The short-term reaction of peatland vegetation to changes in climate depends on the peatland developmental stage, biodiversity, and the current climatic conditions of the site. Co-existing species may often have a more decisive impact on climate change-induced shifts in peatland vegetation than climate change itself. Bog and fen vegetation will react differently to increased temperature and changes in water availability. It seems that the common feature for both major groups of peatlands is the spreading of vascular plants at the expense of *Sphagnum* spp. With the changing climate, graminoids are becoming more abundant in fens and shrubs in bogs (more elaborated in Section 3 Changes in peatland vegetation composition; Fig. 1). Despite that, peatland plant communities are in general resilient and can adapt to steady changes in climate. However, climate extremes like heat and drought waves, with the projected increasing occurrence, present a considerable danger to biodiversity and ecosystem functions of northern bogs and fens.

The changes in peatland vegetation phenology and composition will ultimately impact climate change through altered carbon dioxide and methane fluxes (Fig. 1). The decreasing abundance of *Sphagnum* spp. together with increased shading by larger vascular plant cover will result in lower carbon fixation by peat mosses and probably also by associated phototropic microorganisms. However, this decrease will be lower than the increasing carbon fixation by spreading vascular plants and their longer vegetation period, and the climate change will very likely result in higher carbon fixation by plants (Section 4.1 Carbon fixation).

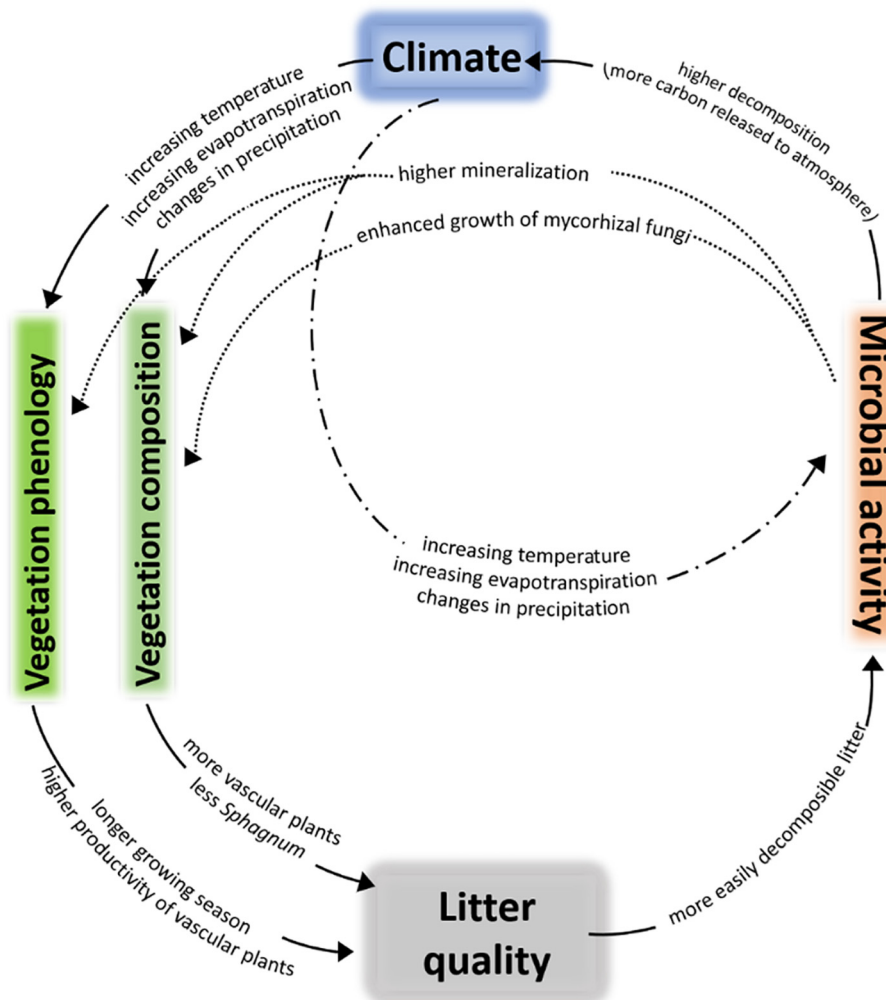


Fig. 1. Climate change-induced changes in peatland vegetation phenology and composition alter climate change.

Peatlands accumulated a vast amount of carbon because of anoxic conditions and litter of poor quality for microbial decomposition. However, the quality of litter input will change together with changes in vegetation composition. Higher decomposition is expected in fens than in bog. An increase in graminoid litter input will create peat with lower polyphenols content together with more suitable carbon: nitrogen and cellulose: lignin ratios for faster microbial decomposition. Shrubs' encroachment of bogs will also alter the litter quality to easier-decomposable, but the presence of woody elements will lower the decomposition rate. The increasing carbon release from bogs will also be caused by increasing colonization by mycorrhizal fungi associated with shrubs. Increased input of simple carbon molecules via root exudates of vascular plants will further increase the number and activity of microorganisms in future peatlands (Section 4.2 Respiration; Fig. 1).

Wetlands, including peatlands, are one of the largest emitters of methane. It is very likely that there will not be significant changes in methane release from bogs in the future. However, due to decreasing water table level and increasing oxidation of the upper layer of peat by shrub roots, methane release from bogs may decrease. Future methane emissions from fens will depend on the water regime. Methane release will increase from fens with an increasing or stable level of the water table due to litter of higher quality, more easily decomposable carbon from root exudates, and more aerenchyma present with a higher abundance of graminoids, which will provide the direct way for methane to escape from deeper layers without being exposed to the oxidative environment of upper layers of peat. Changes in methane release from drier fens are not completely clear, but it is possible that drier fens will release less methane due to thicker acrothelm inhabited by methanotrophic bacteria. The amount of produced and released methane will depend on dominant graminoid species of fens or peatlands in general (Section 4.3 Methane release; Fig. 1).

A special case are peatlands lying at the edge of the permafrost region. Such peatlands are expected to experience dramatic changes once the temperature increases enough to thaw the ice. The plants will start to fix more carbon via photosynthesis, but higher microbial activity will cause higher greenhouse gases, especially methane, release (discussed in Section 4.1 Carbon fixation).

Despite higher carbon uptake from the atmosphere by plants, based on up-to-date knowledge, the result of climate-induced changes in peatland vegetation phenology and composition will be lower carbon accumulation by peatlands in the short term with possible becoming of carbon source in the long term (Section 4 Impact of changes in peatland vegetation on carbon balance).

Although decades of research on climate change impact on peatlands and the possible feedback were conducted, some important information is still missing, which brings uncertainties to predictions about the future climate:

- only the impact of climate change on generative propagation, root, and leaf development was assessed, but the information about the impact of climate change on vegetative reproduction has not been directly studied. The increasing abundance of vascular plants has been reported, but the way of their spreading has not been studied.
- there is no study directly assessing the impact of climate change on *Sphagnum* spp. phenology such as length of growing period or length of photosynthetic activity in natural conditions. Considering the large role of *Sphagnum* spp. in environmental conditions creation and maintenance and carbon storage, this knowledge gap should be addressed. The use of automatization and remote sensing may be necessary to collect frequent enough data for such purpose.
- the biggest threat for peatland plants is not a gradual climate change but the increasing occurrence of climate extremes. There is still relatively little information about the effect of drought and heat waves or extreme precipitation events, especially about their long-term and cumulative effect. There is a need for more information about the mid-term (5–10 years) effect of such events and the resilience of peatland vegetation.

The general trends, which can be expected in this century, are outlined thanks to the decades of work of researchers from many countries cited in this review. However, as humankind, we need more information to make

more precise predictions about the future climate and the point in carbon concentration or temperature increase, which cannot be exceeded to not start unstoppable loops of positive feedback.

CRedit authorship contribution statement

Michal Antala: Conceptualization, Formal analysis, Investigation, preparation of the first draft; **Radosław Juszczak:** Review and editing, Funding acquisition; **Christiaan Van der Tol:** Review and editing; **Anshu Rastogi:** Conceptualization, Formal analysis, Investigation, Funding acquisition, editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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